FOUNDATIONS OF SILVICULTURE

UPON AN ECOLOGICAL BASIS

By The Late JAMES W. TOUMEY

and

CLARENCE F. KORSTIAN

Seeding and Planting in the Practice of Forestry

A manual for the guidance of forestry students, foresters, nurserymen, forest owners, and farmers. *Third Edition*, 1942. Cloth, 6 by 9 inches, 520 pages, illustrated.

Foundations of Silviculture upon an Ecological Basis

A manual for foresters and ecologists, treating of forest vegetation and the various external factors which act upon it. *Second Edition, Revised*, 1947. Cloth, 6 by 9 inches, 468 pages, 20 illustrations.

FOUNDATIONS OF SILVICULTURE

UPON AN ECOLOGICAL BASIS

BY

THE LATE JAMES W. TOUMEY, M.A., D.F., SC.D.

Professor of Silviculture, Yale University

SECOND EDITION, REVISED

BY

CLARENCE F. KORSTIAN, M.F., M.A., PH.D.

Professor of Silviculture and Dean, School of Forestry

Duke University

JOHN WILEY & SONS, INC., NEW YORK

CHAPMAN & HALL, LIMITED, LONDON

1947

SECOND EDITION, REVISED

Second Printing, July, 1948

PRINTED IN THE UNITED STATES OF AMERICA

PREFACE

TO THE SECOND EDITION, REVISED

Before his death in 1932, Professor Toumey suggested that a revision of *Foundations of Silviculture* be undertaken. In the revision, an effort was made to retain as much of his original material as recent advances in forestry, ecology, and plant physiology would justify. These advances made it necessary to reorganize and rewrite some of the chapters and to add new material. No attempt was made to cover all the recent advances; rather, material that was illustrative of particular principles to be emphasized was selected. This revision constituted the second edition of the book. In the present volume, the second edition has been corrected and brought up to date.

Teachers using this book as a textbook in courses in silvics will find it desirable to suggest at least one year of botany, including plant physiology, as a prerequisite to their course or, as a much-less-desirable alternative, a review of this field during the progress of their course.

The literature citations have been arranged alphabetically in the bibliography that follows the last chapter to make them more useful to advanced students and research workers.

One who undertakes a general survey in a subject which is based on so many closely related natural sciences is continually impressed by his own limitations and by the need for the wise counsel of others. Therefore I am glad to express my gratitude to certain of my colleagues for reviewing portions of the manuscript and for their helpful and constructive suggestions. I am especially grateful to Professor T. S. Coile, Professor William Maughan, Dr. H. L. Shirley, Dr. A. S. Pearse, Dr. P. J. Kramer, Dr. E. S. Harrar, Dr. H. J. Oosting, F. W. McIntosh, Dr. A. B. Hatch, and Catherine D. Korstian.

CLARENCE F. KORSTIAN

DURHAM, NORTH CAROLINA
April, 1947

PREFACE

TO THE FIRST EDITION

It is with a measure of hesitation that I send the manuscript for this volume to the printer. I realize the limitations imposed on one who attempts the exposition of forest vegetation in a country as large and as diverse as the United States from the standpoint of the causes which bring it into existence. Although the intensity and duration of the various factors of the site can be known and measured and although the vegetation itself, to a degree, is amenable to instrumentation, we are very far indeed from methods of perfect interpretation of cause and effect.

Although silvics, the American term for foundations of silviculture, lies at the very foundation of silvicultural practice, in comprehensive treatment it has received only scant recognition in the literature of forestry.

The interpretation of cause and effect is the basic reason for all studies of natural phenomena. Darwin's theory of natural selection is based on the adaptation of organism to environment. From the very beginning of silvicultural practice, down to the present time, foresters have been keenly alive to the effect produced on forest vegetation by soil and climate. Foresters in Cotta's day and earlier were accounting for differences in forest vegetation by differences in the intensity and duration of the various factors which are the causative agents to which forests of different kinds are the response.

In the evolution of the subject, the vast body of accumulated facts which gradually came into being, relating to trees and their environment, though useful in silvicultural practice lacked for a long time the following basic concept: *Forest vegetation is composed of plant communities or units of vegetation, developed and arranged in accordance with definite biological laws and is not an aggregation of trees and other plants brought together by chance.*

Our point of view toward silvical research has gradually changed. The collecting of information by observation, although still practiced and useful, is giving way to more accurate methods. *Foundations of Silviculture*, as we conceive it today, is not an outgrowth of plant ecology but rather plant ecology is an outgrowth of it. When biologists took their investigations of the relation of plants to the environ-

ment from the laboratory to the field, they found the silviculturist already there with the accumulated facts of a century of field work. Instrumentation has already been employed in studying the influence of the forest upon local climate and in studying the effects on the forest produced by the site factors. Physical and chemical analyses of forest soils have been made, and transects (under the name of line surveys) and quadrats (under the name of sample plots) have been employed in studying the origin and development of forest vegetation. Although, under another name, this work was in what is now recognized as the field of forest ecology. Foresters were working out their problems because of their importance in silviculture.

Under the leadership of such men as Cotta, Hartig, Koenig, and Pfeil, silviculture began to break away from its empirical basis and to find a foundation in the underlying sciences early in the nineteenth century. Even before this time, Duhamel du Monceau in France and Enderlin in Germany had appreciated the need of lifting silviculture from the rule of empiricism and placing it on a sound scientific foundation. Thus, as early as 1767, Enderlin published a treatise on the characteristics of forest trees and of forest soils in which he described the nourishment of trees and the causes of growth. Although this work was based upon observation and speculation, it pointed the way toward the scientific foundation of later work. *Verhalten der Waldbäume gegen Licht und Schatten* by G. Heyer, published in 1852, is probably the earliest attempt to analyze, in a comprehensive manner, a site factor operating in the forest. It is a classic in which for the first time the theory of tolerance, upon which is built so much of our silvicultural practice, is systematically developed.

The steady but consistent progress made in relating the site factors to forest vegetation is exemplified more recently in the works of Mayr, Duesberg, Wagner, Wiesner, Reuss, Dittmar, Knuchel, Ramann, Rubner, and others, who have applied the fundamental sciences, such as biology, physics, and chemistry, to the theory of silvicultural practice.

In 1861, forest experiment stations were recommended by Ebermayer, and the establishment of such stations during the past half century in all countries where forestry is practiced has been the final step in putting the foundations of silviculture on a firm, scientific basis. These stations are developing the experimental phases of silviculture; they are bringing in the era of modern silvics.

In 1866, Hæckel defined "œcology" as the science that treated the reciprocal relations of organisms and the external world. Until recent times, what is now conceived as ecology was included under biology.

Biology is a general term including both botany and zoology, and ecology is a part of each. Although biologists have for many years been concerned with the relation of plants to their environment, the term plant ecology has come into use within comparatively recent times. As a science, it is a branch of botany which is concerned with the relations of the individual plant, the species, and the plant community to the site. It has its roots firmly anchored in the basic principles of physics, chemistry, physiology, geology, and meteorology.

The first important step in the development of plant ecology as a distinct department of botanical science was the recognition by Grisebach in 1838 that the plant community is a fundamental unit of vegetation. This basic concept has been accepted by silvicists and has been used by them in the classification of forest vegetation and in the demarcation of forest types. Since the time of Grisebach, other botanists, among whom may be mentioned de Candolle, Schouw, Engler, von Humboldt, Drude, Schimper, and Warming, contributed generously to early ecological knowledge. More recently experimental plant ecology has been undertaken by Bonnier, Moss, Tansley, Solms-Laubach, and many others in Europe and by Clements, Cowles, Shreve, Fuller, Boerker, Sampson, Weaver, Nichols, Bates, Zon, and others in the United States.

The methods of the silviculturist in the process of being worked out at forest experiment stations were seized upon by the plant ecologist, and instrumentation was developed for the measurement of the intensity and duration of the site factors. Transects and quadrats were laid out after the fashion of the line survey and sample plot of the forester.

The researches in plant physiology as illustrated by the work of Livingston, Burns, and Shantz in this country, where the investigations are taken from the laboratory to the field, have been of incalculable help to the ecologist and forester alike in developing practical methods for measuring the intensity and duration of action of site factors.

With the development of experimental plant ecology in the latter part of the nineteenth century, the work of the forester and the work of the ecologist came together, both searching by means of experimentation for the fundamental laws underlying the relation of vegetation to site. The field of the plant ecologist and the field of the forester differ chiefly in magnitude and in the application of the results. Although the student of silviculture has gained immeasurably from the ecological concept, the entire foundations of silviculture can not be relegated to ecology.

The great advantage of the ecological concept toward biological forest facts, useful in the understanding of the forest and to serve as a foundation for the practice of silviculture, lies in the recognition of forest communities and in the appreciation that they are not fixed units but are in a constant state of change. Ecology is of fundamental importance to the forester because it brings a true scientific attitude to the multitudinous problems bearing upon the origin and development of forests. The silviculturist studies the forest in order to assemble scientific facts useful in their economic application to the production of timber. The most comprehensive study of environmental factors by the forester leads to nothing useful, unless the forest vegetation itself is interpreted in harmony with them.

In order to make this manual pedagogical and as simple in treatment as the subject permits, it is divided into two parts, namely, Part I, *The Site Factors;* and Part II, *The Forest Vegetation.* Under the first are presented the various external factors which act upon forest vegetation and the modifications in the vegetation that are due to their action. Here also are discussed the various reactions of forest vegetation on these factors. Under the second are presented an analysis of the forest, the units of forest vegetation, their origin and development under the action of the site factors, and the biology of the stand and the individual.

From the nature of the work, I have drawn from many sources. My own researches have been utilized wherever possible. The greater part of the material, however, is drawn from the voluminous silvicultural literature of the past and from modern researches in plant ecology. The originality that I claim is chiefly in the manner of assembling the material and in bringing together the researches of the forester and the ecologist in a manner which I hope will serve a useful purpose as a foundation for the practice of American silviculture.

I am under obligations to many American foresters and plant ecologists for advice and assistance. The manuscript in its entirety or in part has been reviewed and criticized by Dr. C. F. Korstian, to whom I owe a special debt of gratitude, Barrington Moore, Dr. G. E. Nichols, G. A. Pearson, Professor S. N. Spring, and Professor J. A. Larsen. The chapter on solar radiation as a site factor has been reviewed and criticized by Dr. A. Grasovsky and the chapters on soil factors by Professor M. F. Morgan.

J. W. Toumey

Yale University,
September 1, 1928

CONTENTS

CHAPTER I

INTRODUCTION — DEFINITIONS AND GENERALITIES

1. Foundations of Silviculture 1
2. Practice of Silviculture 2
3. Silvical Basis for Rational Silvicultural Practice 3
4. Environment or Site 7
   5. Site Quality 8
   6. Factors of Site (Habitat Factors) 10
      7. Climatic Factors 11
      8. Edaphic Factors 12
      9. Physiographic Factors 12
      10. Biotic Factors 12
   11. Classification of Site Factors Based on Their Mode of Affecting Vegetation 13

PART I. ENVIRONMENT OF FORESTS

CHAPTER II

SOLAR RADIATION

1. Importance 14
2. Radiant Heat and Light 14
   3. Solar Radiation that Reaches Earth's Surface 16
4. Effects of Solar Radiation on Forest Vegetation 17
   5. Effects of Light 17
      6. Light Intensity and Photosynthesis 18
      7. Light Intensity and Growth 23
      8. Changes in Light Quality in Forests 26
      9. Light and the Form and Development of Trees 29
         10. Relation of Light Intensity and Light Quality to Development of Tree Organs 29
         11. Relation of Light Intensity and Light Quality to Phototropic Effects 31
      12. Influence of Light Intensity on Winter Hardiness and Drought Resistance 31
   13. Duration of Radiation and Effects 32
   14. Temperature Effects 33
15. The Light Factor in Silvicultural Practice 35
16. Summary of Radiant Energy in Relation to Forest Vegetation 36

CHAPTER III

AIR TEMPERATURE

1. Sources of a Tree's Heat 40
2. Absorption of Heat by a Tree 40

3. Injurious Effects of Heat 41
4. Injurious Effects of Cold 41
5. Effect of Temperature on Different Plant Functions 42
6. Critical Temperatures for Forest Vegetation 43
7. Lower Critical Temperatures 43
8. Upper Critical Temperatures 45
9. Species in Relation to Critical Temperatures 45
10. Individuals in Relation to Critical Temperatures 46
11. Extension of a Tree's Range 47
12. Air Temperature and Forest Vegetation 47
13. Acclimatization 48

CHAPTER IV

ATMOSPHERIC MOISTURE

1. Water and Vital Processes in Trees 50
2. Precipitation 51
3. Resistance Offered by Trees to Mechanical Injury from Precipitation 54
4. Mechanical Action of Snow on Forest Growth 55
5. Mechanical Action of Sleet and Glaze on Forest Growth 56
6. Atmospheric Humidity 57
7. Effect of Variations in Atmospheric Humidity on Forest Vegetation 59
8. Evaporation 61
9. Ratio of Precipitation to Evaporation 61
10. The Precipitation-Vapor Pressure Deficit Quotient 62

CHAPTER V

CLIMATE

1. Importance of Climate and Weather in Forestry 63
2. Weather 64
3. Sources of Air Masses 64
4. Characteristics of Air Masses 64
5. Highs and Lows 65
6. Air Masses of the United States 65
7. Fronts 66
8. Precipitation 67
9. Storm Paths 67
10. Periodicity in Climate 68
11. Climatic Provinces 69
12. Integration of Climatic Factors 69
13. Wind 71
14. Direct Action of Wind on Forest Vegetation 71
15. Effect of Continuous Stress Caused by Wind 72
16. Windfall and Windbreak 73
17. Resistance of Different Species to Wind 74
18. Indirect Effect of Wind on Forest Vegetation 74
19. Effect of Wind on Distribution of Forests 75
20. Utility of Wind to Trees 75
21. Lightning 76
22. Direct Effect of Lightning on Forests 77
23. Indirect Effect of Lightning on Forests 77
24. Carbon Dioxide Content of Forest Air 78

25. Atmospheric Impurities 78
26. Resistance to Injury from Atmospheric Impurities 79

CHAPTER VI

SOIL CONDITIONS

1. Soil in Relation to Trees 80
2. The Soil Profile 81
3. Weathering Processes 82
4. Processes of Soil Development 83
5. Podsolization 83
6. Laterization 84
7. Calcification 85
8. Soil Classification 86
9. Physical Nature of Soil 88
10. Soil Structure 89
11. Volume Weight 91
12. Depth of Soil 91
13. Inorganic Chemical Nature of Soil 91
14. Base Exchange 92
15. Nature of Soil Organic Matter 93
16. Forest Humus Types 94
17. Effect of Humus on Forest Vegetation 95
18. Sources of Available Nitrogen in Forest Soils 96
19. Physical Effect of Organic Matter on Forest Soil 96
20. Forest Soil Acidity (Reaction) 97
21. Soil Characteristics and Height Growth 98
22. Effect of Fire on Forest Soil 99
23. Microorganisms in Forest Soil and Their Relation to Soil Fertility 100
24. Plant Life in the Soil 100
25. Mycorrhizae 102
26. Types of Mycorrhizae 103
27. Prevalence of Mycorrhizae in Trees 103
28. Rôle of Mycorrhizae in Tree Nutrition 104
29. Animal Life in the Soil 106
30. Soil Structure and Soil Fertility 107
31. Soil Temperature 108
32. Shrinking and Swelling of Soil Under Action of Frost 110
33. Fluctuations in Soil Temperature 111
34. Influence of Soil Temperature on Form of Forest Vegetation 111
35. Soil Temperature in Forests as Compared with the Open 112
36. Soil Atmosphere 113
37. Adjustments to Poorly Aerated Soils 114
38. Effect of Filling in Around Trees on Aeration 115
39. Toxic Soil Gases 116
40. Effect of Silvicultural Practice on Soil Characteristics 116

CHAPTER VII

SOIL MOISTURE AND ITS INFLUENCE ON FOREST VEGETATION

1. Basic Concepts 120
2. Movement of Soil Moisture 121
3. Soil Moisture Constants 123

4. Water Percolation in Soil 125
5. Loss of Water from Soil 125
6. Water Loss through Evaporation 126
7. Water Loss through Transpiration 127
8. Absorption of Soil Water by Trees 131
9. Water Supply of Forest Soils 132
10. Fluctuations in Available Water in Forest Soils 134
11. Influence of Available Soil Moisture on Forest Vegetation 135
12. Adjustments to Available Soil Moisture 137
13. Adjustments for Control of Water Loss 138
14. Variations in Internal Structure 138
15. Variations in Area of Evaporating Surface 139
16. Variations in Illumination of Assimilating Organs 140
17. Variations in Epidermal Outgrowths and Coverings 140
18. Variations in Shoot Form, Particularly in Height Growth 141
19. Adjustments for Control of Water Intake 141
20. Variations in Internal Structure 141
21. Variations in Osmotic Pressure of Sap 142
22. Variations in Area of Root Surface as Compared with Shoot Surface 143
23. Variations in Root Habit and Root Form 144
24. Variations in Root Habit as Expressed in Adult Trees 145
25. Plasticity in Initial Root System 145
26. Correlation Between Rapidity of Juvenile Root Penetration and Surface Desiccation of Soil 147
27. Depth of Root Penetration in Relation to Available Soil Moisture 147
28. Characteristic Forms of Initial Root Habit and Their Relation to Available Soil Moisture 148
29. Species with Long Initial Taproots and without Prominent Laterals 148
30. Species with Short Initial Taproots and Prominent Laterals 150
31. Species with Long Initial Taproots and Prominent Laterals 151

CHAPTER VIII

PHYSIOGRAPHIC CONDITIONS

1. Earth Configuration 154
2. Altitude 155
3. Slope 158
4. Exposure 159
5. Surface Conditions 161
6. Non-living Soil Cover 161
7. Snow 161
8. Forest Litter 163
9. Living Soil Cover 163

CHAPTER IX

BIOTIC FACTORS

1. Competition 164
2. Interrelationships between Plants 166

3. Importance of Plant Parasites.................................. 169
4. Effects of Animals.. 171
5. Domestic Grazing Animals...................................... 172
6. Deer and Elk.. 174
7. Beaver.. 174
8. Rabbits... 175
9. Squirrels... 175
10. Porcupines.. 176
11. Mice... 176
12. Birds.. 176
13. Insects.. 177
14. Interference by Man... 177
15. Agriculture.. 179
16. Lumbering.. 179
17. Introduction of Plants and Animals.......................... 179
18. Introduction of Pests.. 180
19. Fire.. 180

CHAPTER X

INTERACTION OF SITE FACTORS

1. Measuring Effectiveness of Site Factors...................... 182
2. Effect of Site Factors on Forest Vegetation.................. 183
3. Compensating Factors... 183
4. Most Significant Factors....................................... 186
5. Modification of Site Factors in Silvicultural Practice........ 189

PART II. INFLUENCE OF FORESTS ON THEIR ENVIRONMENT

CHAPTER XI

REACTION OF FOREST VEGETATION ON ITS PHYSICAL ENVIRONMENT

1. Reaction Concepts.. 193
2. Classification of Forest Reactions............................ 194
3. Effect of Forest Vegetation on Air Temperature................ 194
4. Effect of Forest Vegetation on Soil Temperature............... 198
5. Effect of Forest Vegetation on Atmospheric Humidity........... 201
6. Effect of Forest Vegetation on Precipitation.................. 204
7. Effect of Forest Vegetation on Local Precipitation............ 205
8. Effect of Forest Vegetation on General Precipitation.......... 206
9. Effect of Forest Vegetation on Conservation of Water.......... 207
10. Effect of Forest Vegetation on Evaporation.................. 207
11. Evaporation from Tree Crowns.............................. 208
12. Evaporation from the Ground............................... 210
13. Effect of Forest Vegetation on Transpiration Loss........... 212
14. Effect of Forest Vegetation on Surface Runoff............... 213
15. Effect of Forest Vegetation on Seepage and Water Retention.... 215
16. Effect of Forest Vegetation on Springs....................... 216
17. Effect of Forest Vegetation on Stream Flow.................. 217
18. Effect of Forest Vegetation on Floods....................... 220

19. Effect of Forest Vegetation on Air Currents.......... 221
20. How Windbreaks Act.......... 222
21. Effect of Windbreaks on Air and Soil Moisture.......... 222
22. Effect of Windbreaks on Temperature.......... 223
23. Effect of Forest Vegetation on Avalanches.......... 224
24. Kinds of Avalanches.......... 224
25. Relation of Forest Cover to Ground and Top Avalanches.......... 225
26. Effect of Forest Vegetation on Soil.......... 226
27. Effect of Forest Vegetation on Wind Erosion.......... 226
28. Effect of Forest Cover on Water Erosion.......... 227
29. Methods of Preventing and Overcoming Damage from Water Erosion.......... 228

CHAPTER XII

EFFECT OF FORESTS ON ANIMAL LIFE, PARTICULARLY MANKIND

1. Effect of Forests on Animal Life.......... 229
2. Forests as Source of Food for Animals.......... 229
3. Forests as Environments for Animals.......... 230
4. Effect of Forests on Mankind.......... 232
5. Influence of Forests on Civilization.......... 233
6. Sanitary Influence of Forests.......... 233
7. Favorable Effect on Amelioration of Weather.......... 234
8. Favorable Effect on Reduction of Pathogenic Microbes.......... 234
9. Favorable Effect on Potable Water.......... 235
10. Favorable Effect on Tranquility of Mind.......... 236
11. Forest Aesthetics.......... 236
12. Foundations of Forest Aesthetics.......... 237
13. Applied Forest Aesthetics.......... 238

PART III. FORESTS

CHAPTER XIII

FORM AND LIFE OF FOREST TREES

1. Structures and Functions.......... 239
2. Species, Varieties, Races, and Individuals.......... 240
3. Species.......... 241
4. Varieties.......... 241
5. Sport Varieties and Sport Forms.......... 241
6. Races.......... 242
7. Individuals.......... 243
8. Hybrids and Cross-breeds.......... 244
9. Tree Form.......... 244
10. Form of Crown.......... 245
11. Deviations from Typical Crown Form.......... 246
12. Effect of Age on Crown Form.......... 247
13. Form of Bole.......... 247
14. Straightness of Bole.......... 247
15. Taper of Bole.......... 248
16. Cross-sectional Form of Bole.......... 248

17. Deviations in Bole Form Due to Restrictions in Growing Space 248
18. Deviations in Bole Form Due to Age 248
19. Deviations in Bole Form Due to Site 249
20. Bole Excellencies and Bole Defects 249
21. Inherent Characteristics 249
22. External Influences 250
23. Crotched or Double-topped Trees 251
24. Epicormic Branches and Water Sprouts 251
25. Stool Shoots and Coppice Shoots 252
26. Form of Roots 253
27. Inherent Characteristics 253
28. External Influences 253
29. Growth and Development 254
30. Periods of Rest 256
31. Growth Rings 258
32. Longevity and Death 259
33. Classification of Species and Varieties on Basis of Duration of Growth 261
34. Determining Age of a Tree 261
35. Rapidity of Growth 262
36. Classification of Species and Varieties on Basis of Growth Energy 263
37. Growth Characteristics of Chief Importance 263
38. Height Growth 264
39. Determinate Growth in the Leading Shoot 264
40. Indeterminate Growth in the Leading Shoot 265
41. Annual Height Growth 265
42. Maximum Height 266
43. Diameter Growth 267
44. Effect of Age on Diameter Growth 267
45. Variations in Diameter Growth in Different Parts of a Tree 268
46. Taper Change 270
47. Volume Increase 270
48. Quality Growth 270
49. Reproduction 271
50. Seed Production 272

CHAPTER XIV

DIFFERENTIATION AND DEVELOPMENT OF STANDS

1. Differentiation of Stands 275
2. Differentiation of Stands on Basis of Age of Component Elements 275
3. Developmental Stages in Stands 276
4. Character and Form of an Even-aged Stand 277
5. Advantages of Even-aged Condition of Stand 278
6. Disadvantages of Even-aged Condition of Stand 279
7. Differentiation of Stands on Basis of Composition 279
8. Pure and Mixed Natural Stands 281
9. Occurrence 281
10. Mixtures by Individuals and by Groups 282
11. Fundamental Principles Underlying Natural and Artificial Composition of Stands 282

12. Differences in Reaction of Pure and Mixed Stands.............. 284
13. Formative Ability of Different Species When in Stands.......... 285
14. Directing Composition of Stands................................ 286
15. Pure Stands as Compared with Mixed.......................... 287
16. Dependent Species in Pure Stands............................... 288
17. Advantages of Pure Stands..................................... 289
18. Advantages of Mixed Stands When Correctly Made and Maintained... 290
19. Even-aged Artificial Mixtures.................................. 296
20. Two-aged Artificial Mixtures................................... 297
21. Temporary Mixtures.. 298
22. Differentiation of Stands on Basis of Density.......................... 299
23. Crown Closure.. 299
24. Degree of Crown Density in Stands........................ 299
25. Conditions which Influence Crown Density.................. 301
26. Importance of Crown Closure and Its Influence on Life of a Stand.. 301
27. Crown Closure and Growth................................ 303
28. Crown Closure and Soil Quality........................... 304
29. Crown Classification.. 304
30. Crown Classification for Even-aged Stands.................. 304
31. Dunning's System of Crown Classification for Uneven-aged Stands.. 306
32. Root Closure.. 308
33. Effect of Root Closure on Life of a Stand.................. 309
34. Conditions which Influence Density of Boles...................... 310
35. Development of Stands.. 311
36. Development of Even-aged Stands.............................. 311
37. Development of Uneven-aged Stands............................ 314
38. Development of Sprout Stands.................................. 316

CHAPTER XV

REPRODUCTION, GROWTH, AND YIELD OF STANDS

1. Reproduction of Stands.. 317
2. Natural Reproduction.. 317
3. Origin of Natural Reproduction............................ 318
4. Conditions Under which Natural Reproduction Can Not be Attained.. 318
5. Methods of Natural Reproduction from Seed................ 319
6. Selection Method...................................... 319
7. Shelterwood Method.................................. 319
8. Seed-Tree Method..................................... 320
9. Clear-cutting Methods 320
10. Clear-cutting in Strips............................. 321
11. Clear-cutting in Patches............................ 321
12. Successful Natural Reproduction from Seed.................. 321
13. Continuous and Discontinuous Reproduction................ 322
14. Problems of Natural Reproduction.......................... 322
15. Reproduction in Clearings............................. 322
16. Reproduction within Stands............................ 324
17. Study of Natural Reproduction............................ 325
18. Effect of Fire on Natural Reproduction.................... 326
19. Effect of Lumbering on Natural Reproduction.............. 327

20. Effect of Grazing on Natural Reproduction.................. 328
21. Growth of Stands.. 329
22. Increment in Stands.. 329
23. Effect of Thinning on Growth.................................. 330
24. Yield of Stands.. 331
25. Factors Affecting Yield of Stands................................ 332

CHAPTER XVI

TOLERANCE

1. Concept of Tolerance.. 336
2. Definitions of Tolerance.. 341
3. Methods of Determining Tolerance.................................. 341
4. Direct Methods of Determining Tolerance........................ 342
5. Indirect Methods of Determining Tolerance..................... 343
6. Density of Crown.. 343
7. Natural Pruning.. 344
8. Number of Branch Orders.................................... 344
9. Natural Thinning of Stand.................................... 345
10. Condition of Reproduction.................................... 345
11. Relative Height.. 346
12. Cambium-crown Surface Ratio.............................. 346
13. Artificial Shading.. 346
14. Leaf Structure.. 347
15. Rate of Height Growth...................................... 347
16. Factors Influencing Tolerance.................................... 347
17. Temperature.. 347
18. Altitude 348
19. Scales of Tolerance.. 349
20. Silvicultural Importance of Tolerance.......................... 353

CHAPTER XVII

FOREST VEGETATIONAL UNITS AND THEIR CLASSIFICATION

1. Concepts.. 356
2. Cause and Effect.. 356
3. Classification of Vegetation.................................... 357
4. Classification of Vegetation on Basis of Growth Form...... 358
5. Natural Vegetational Areas.................................... 358
6. Forest Vegetational Areas in United States.......................... 359
7. Forest Vegetational Areas on a Non-ecological Basis.............. 359
8. Brewer's Classification.................................... 359
9. Sargent's Classification.................................... 359
10. Merriam's Classification.................................. 360
11. Mayr's Classification...................................... 361
12. United States Forest Service Classification.................. 362
13. Forest Vegetational Areas on an Ecological Basis................ 365
14. Clements' Classification.................................. 368
15. Shreve's Classification.................................... 368
16. Zon's Classification.. 370
17. Forest Communities of Varying Degrees of Magnitude.............. 373
18. Forest Formation.. 373
19. Climatic Forest Formation.................................... 374

20. Physiographic Forest Formation.... 375
21. Development of Forest Formations.... 375
22. Delimiting Forest Formations.... 376
23. Forest Association.... 377
24. Forest Types.... 379
25. Concepts of Forest Types.... 380
26. Cover Type.... 382
27. Permanent Type.... 382
28. Temporary Type.... 382
29. Physical Type.... 382
30. Management Type.... 383
31. Indicator Type.... 383
32. Relation of Forest Types to Ecological Units.... 383
33. Usefulness of Type Concepts.... 385
34. Application of Cover Types.... 385
35. Examples of Regional Classification of Cover Types.... 386
36. Application of Management Types.... 390
37. Application of Physical Types.... 391
38. Application of Temporary and Permanent Types.... 392
39. Application of Indicator Types.... 392
40. Delimiting Types.... 395

CHAPTER XVIII

ORIGIN AND DEVELOPMENT OF FOREST COMMUNITIES: FOREST SUCCESSION

1. Concept of Succession.... 396
2. Primary and Secondary Series in Succession.... 397
3. Secondary Succession Following Denudation by Burning.... 397
4. Secondary Succession Following Denudation by Lumbering.... 398
5. Initial Causes in Succession.... 398
6. Continuing Causes in Succession.... 399
7. Plant Grouping.... 399
8. Variety in Grouping.... 400
9. Grouping in Response to Light and Moisture.... 401
10. Relation of Grouping to Structure in Forest Vegetation.... 402
11. Zonation.... 402
12. Alternation.... 403
13. Plant Movement and Establishment.... 403
14. Migration.... 404
15. Degree of Mobility in Migrants.... 405
16. Agents for Carrying Migrants.... 405
17. Nearness of Parent Area to New Locality.... 407
18. Topography in Intervening Country.... 408
19. Direction of Movement.... 408
20. Establishment.... 408
21. Germination.... 409
22. Growth and Development.... 411
23. Reproduction.... 412
24. Competition and Reaction.... 412
25. Competition.... 413
26. Competition for Moisture.... 413
27. Importance of Competition.... 414

28. Reaction 415
29. Classification of Reactions 415
30. Soil Reactions 415
31. Recognition of the Climax in Succession 416
32. Direction Taken by Succession: Retrogression 416

APPENDIX: COMMON AND TECHNICAL NAMES OF TREES 419

BIBLIOGRAPHY 425

INDEX 459

CHAPTER I

INTRODUCTION — DEFINITIONS AND GENERALITIES

Silviculture is that branch of forestry which deals with the establishment, development, care, and reproduction of stands of timber. Its aim is the continuous production of wood. Silviculture may be divided into two logical and natural parts:

1. The foundations of silviculture, the scientific basis.
2. The practice of silviculture, the application of the scientific basis.

1. FOUNDATIONS OF SILVICULTURE

Much information about the life of trees and of entire forests has been accumulated, more particularly in recent years. This knowledge has been acquired by direct observation, and by experimentation, that is, by measuring the environmental conditions and by measuring the vegetation. When arranged and classified, this knowledge is the scientific basis for the practice of silviculture. It aims to interpret forest vegetation as influenced by its environment, that is, by the factors of the habitat, such as climate, soil, and animal life. This body of information is a science insofar as it establishes relationships and becomes the basis for laws which are generally true regarding forests. As the principles which it teaches gradually came to light they were brought together under the term *foundations of silviculture* (Schlich, 1896).[1] Fernow (1902) used the term *biological dendrology.* Later both Fernow (1905) and the U. S. Forest Service accepted the term *silvics* for that part of silviculture which is the scientific basis for its practice. *Silvics* has been defined as (1) *that branch of ecology which treats of the life of trees in forests* and (2) *the life history and general characteristics of forest trees and stands, with particular reference to environmental factors* (Soc. Amer. Foresters, 1944). The first definition is essentially synonymous with *forest ecology* and the second with *silvicultural characteristics.*

Silvics emphasizes the concept that a forest has structures and

[1] When an author's name is followed by a date, the full reference will be found in the Bibliography, pp. 425–457.

functions capable of exact methods of study. It teaches the why rather than the how of silviculture. Silvics concerns a forest, not as a mere aggregation of trees like so many stones in a field but as a complex structure composed of units of vegetation. Each of these is an integral biological unit differing from other units because the combined effect of the habitat factors is different. A thorough understanding of silvics enables foresters to relate forest vegetation to its habitat and also enables them to interpret the effect of forest vegetation on its environment. Silvics considers the summation of the effects of various environmental factors which represents the yield capacity of an area of forest land. Thus the quality of a habitat depends upon the environmental factors. Foresters must know how the various habitat factors act upon forests in order to practice silviculture without serious mistakes under any given combination of factors. Through them the actual growth capacity of a forest stand is known.

An understanding of silvics is a prerequisite to the practice of silviculture. Although much information concerning the life of trees and forests has already been obtained, much more is still needed in order fully to correlate the interacting factors, to establish the various relationships, and to determine the basic natural laws governing reproduction, growth, and development of forests. Silvics is thus still in its infancy insofar as it is concerned with supplying adequately the specific information necessary to solve the many important problems in silviculture.

2. PRACTICE OF SILVICULTURE

The practice of silviculture deals with the various methods of raising and caring for forest crops. It is applied silvics. It is concerned with the intimate relation which exists between the various methods of cutting a stand and the natural regeneration which is expected to follow under various favorable and adverse environmental conditions. It explains the operation and application of the various silvicultural systems developed to obtain regeneration and the conditions essential for the success of each. The aim of each method of natural reproduction is complete restocking by natural means as a consequence of the method of removal of the old stand. It deals with the different methods for tending and caring for stands and explains the methods leading to the improvement in the form of bole and crown. It is concerned with cleanings, prunings, thinnings, cuttings, and other treatments designed to improve the quantity and quality of existing stands, and with the applicability and advantages of the different methods. For

detailed discussions of the silvicultural treatment of forest stands the reader should consult special works on this subject such as those by Troup (1928), Möller (1929), Dengler (1935), Westveld (1939), and Hawley (1946). The practice of silviculture also includes the collection of forest-tree seed, nursery practice, and artificial reforestation for timber production and other purposes (Toumey and Korstian, 1942).

The essentials of modern applied silviculture can be characterized by four words: soil, reproduction, pruning, and thinning. By combining the influence of all four in rational silvicultural practice the highest quality and quantity of timber may be produced, thus attaining maximum financial returns while maintaining the soil at its highest productive capacity.

3. SILVICAL BASIS FOR RATIONAL SILVICULTURAL PRACTICE

A natural, unmanaged wild forest, in all stages of its development from a denuded area to one covered with climax vegetation, is the field where the underlying silvical principles that determine sound silvicultural practice must be discovered. It is here that the laws of forest reproduction, growth, and development have their origin. The natural forest, from the time vegetation first starts on a denuded area until the climax forest is attained, is in a dynamic condition of reaction and adjustment. When the climax is finally reached, a forest is in its most stabilized form and the area is most fully occupied. A climax forest is the product of nature toward which the vegetation is always tending, but this progression is frequently interrupted by agencies causing complete or partial upsets or retrogressions.

When man enters a natural forest and works therein to make it of increased economic value, he interferes more or less with the natural adjustment or succession that is in progress in the trend of a forest toward its climax form. This influence may be favorable or unfavorable from a silvical standpoint. It may be unfavorable from a silvical standpoint and favorable from an economic standpoint. Often as a result of his activity there is danger of soil deterioration and of increased damage from external agents and from unfavorable climatic conditions. Although one of the chief aims of silviculture is to increase the economic value of forests, the operations which lead to this increase can not ignore the basic laws of reproduction and growth in natural forests. Study of natural forests should make it possible to foresee what operations can be undertaken in an effort to increase forest revenue without destroying or seriously interfering with the equilibrium

which exists between forest growth itself and climate, soil, and other environmental factors.

The natural history of forests is rapidly becoming known. Until recently there was no definite conception of the real life of a forest. Its origin, its mode of development, and its climax form were matters of speculation without much scientific foundation. Silvicultural studies were chiefly concerned with the character and condition of the crop, the revenue, and the relation of forest vegetation to game.

The more profound a forester's knowledge of the life of forests in all their aspects, the fewer difficulties he encounters in modern practice of silviculture. Unfortunately, however, even under present silvicultural practice, the need for a comprehensive knowledge of forest life itself is not fully appreciated. The study of silvics, both in forestry schools and by practitioners in the field, should be encouraged.

In the forestry schools and in practice overemphasis is often placed upon the simple, practical silvicultural activities, and the foundations of silviculture derived from the study of forest life are ignored. In many cases underlying principles are passed over and students become proficient on diverse working rules, for the most part empirical.

Nature protests with great emphasis against unnatural conditions. When all or a part of a climax stand is removed from a given area, the tendency is for the same kind of stand to be reestablished in time. In the economic improvement of a forest, however, more or less transitory stands must be developed. The moment man cuts in a natural stand or otherwise changes it, the stand becomes in part unnatural. The improvement of stands centers in retaining the more desirable qualities of natural forests, thus obtaining high economic value. The application of fundamental biological principles in silvicultural practice is often difficult and the resulting success depends upon a knowledge of the natural history of a forest. With such knowledge it is possible to go forward with comprehension and attain an agreement between natural forests and economic forests. In bringing about this agreement, the importance of forest economics should not be under-rated, nor the silvicultural importance of the underlying natural laws of forest ecology over-rated. Both must be adequately considered. In other words, valid economic principles and basic silvical principles must be coordinated in a silvicultural practice that is both biologically and economically sound.

Natural forests with their variety of species and bole-forms include individual trees of both large and small size and with wide and narrow crowns. When mature the number of upright, symmetrical boles per

unit of area is small. Revenue production by natural forests is acceptable only when their original cost is low.

Rational silvicultural practice then is not the attaining of maximum tree development, but the permitting of trees to live only sufficiently long to become large enough to yield the highest value per unit of area. Reproduction of the larger, older, decadent, and more impressive trees of natural forests is not attempted in artificial forests where special attention is given to obtaining vigorous trees under regulated management.

Although reproduction usually starts quickly in open spaces in natural forests, establishment under cover of an overstory often requires a long period of time. The growth of the young trees is restricted by the shade and root competition of older individuals. As the canopy of old trees becomes broken through injury or death, the young trees are able to make their way through the openings until they finally reach full overhead light. Sometimes 50 to 100 years are required from the time seeds fall from the parent trees until the next crop is ready to harvest. It is impossible for a silviculturist to follow this development. Knowledge of it must be derived from inference, namely, from the study of many similar trees in various stages of development. Foresters from studies of growing trees and stands can foretell the establishment of the new generation and the possibility of reproduction when the old stand is removed from an area.

It is the way of nature that a bare area is more or less rapidly covered with vegetation composed of small-seeded species that bear wind-disseminated seeds. Part of these species are herbs of various kinds, such as weeds and grass; part are shrubs; and a few are trees like aspen, birch, and small-seeded conifers with winged seeds. All of these are present in the field during the first generation. Usually, undesirable species of trees are far more numerous in such fields than all other trees, since these species generally bear seed in abundance. The more desirable trees as a rule bear seed only intermittently and the seedlings are often so delicate that they can survive only where soil conditions are best for germination and survival and where climatic extremes are favorable for their growth and development. Nature scatters seeds of the various species without vision. For example, she often brings ash seed to soil silviculturally hostile to ash.

In nature, the new generation of trees that spreads over an open area is more or less accidental and unrestricted. Finally, this generation of wind-disseminated species, if undisturbed by man or fire, becomes closed and forms a continuous canopy. Various mammals, birds, and

lesser forms of animal life find their home in it, and probably aid in bringing in the heavy-seeded species. In the hardwood forests of the east-central United States the heavy-seeded species gradually become established and ultimately drive out the small, wind-disseminated species.

This slow but definite course through which a forest passes in its natural development can be materially hastened by silvicultural treatment to shape composition and density of the succeeding stand. When a forest is regenerated without the guidance of man, natural selection usually does not produce the tree species desired or in the proportion wanted. It is evident, therefore, that foresters must learn not only how to hasten reproduction but also how to assist nature in bringing into the regeneration the species desired.

When seeds of a given species are distributed beyond its natural geographical range or when trees are artificially introduced from outside, they may grow for a time; but when left to themselves they are usually overwhelmed by the conditions imposed by their new environment. In general the extension of the range of a species beyond its natural habitat is impossible unless it extends into a region of similar climate. Silvics, by teaching the requirements of tree species and the laws of natural distribution, protects practicing foresters against serious mistakes in the choice of species.

Silvics indicates which trees are unable completely to utilize the soil at hand and which trees will develop excellent bole-form under existing site conditions. It offers basic reasons for making a choice between pure and mixed stands for particular sites and shows what species develop best in mixed stands and what the proportion must be in order to attain the required results. Silvics points the way that foresters must follow in protecting forests against damage due to natural causes, such as prevailing wind, lightning-caused fires, insects, and fungi. This protection is afforded by measures taken in the selection of species, in starting a forest, and in its development.

As natural forests offer the greatest resistance to damage from external causes, it is here that foresters must find the foundation pattern for artificial stands. Artificial stands should, so far as possible, conform silviculturally with natural stands, but without their economic disadvantages, owing to irregular reproduction, open crown cover, and poor boles. So far as reproduction is concerned, nature works slowly but inexpensively.

Reproduction, if it is to be obtained at low cost, must be done slowly and with the help of nature. Obtaining reproduction immediately

often means excessive labor and high cost. It is an object of silviculture to find a way to obtain rapid natural reproduction at low cost; otherwise resort to artificial regeneration will be necessary.

The biological principles that silvics imposes upon silvicultural practice must be considered in connection with forest exploitation. The two must work together. The removal of material from a forest should always have a silvicultural aim. As production must be regulated so that its continuation is assured, silvicultural operations must be carried out so as to maintain soil quality, which is the source of all production. A natural forest usually maintains soil quality ideally, even though the forest be deficient in production. The improvement of natural regeneration and the maintenance of soil quality are fundamental requirements of silviculture. On lands where virgin forests have been destroyed, and where the conditions imposed by nature do not permit the natural formation of a new forest within a reasonable time, artificial reforestation is usually necessary.

Owing to the activities of man, large areas of forest in the United States are in need of silvicultural treatment. It is not known at the present time what will ultimately be the accepted silvicultural practice on these areas. It is known, however, that the observations and research needed to determine the practice must be thorough and comprehensive. Through such studies, through an understanding of the natural history of forests, and through logical reasoning from cause to effect, silvics is rapidly taking its place as a science upon which a rational practice of silviculture will in time be built.

4. ENVIRONMENT OR SITE

In considering the foundations of silviculture from an ecological viewpoint, a forest must necessarily be regarded as a definite biological entity composed of innumerable organisms, and its environment, as that of any organism, is the resultant of all the external conditions which influence it. The forest environment, being the complex of conditions that it is, can be understood and the nature of its influence interpreted only by factoring the environment into its various components. The environment of a forest is very commonly referred to by the term *site*. Site as used by foresters is the exact equivalent of *habitat* as used by ecologists. It is equivalent to the term *locality* as used by European writers on silviculture. As a silvical concept, site may be taken to mean the sum of the effective conditions under which a plant or plant community lives (Tansley, 1923). As used by systematists in describing the range of a species, it means the place in

which a plant lives. In addition to its earlier meaning, it has now become a scientific term applied to the combination of climatic and soil conditions affecting a plant, which are incidental to the place in which the plant lives. Nichols (1917) has defined *habitat* as *any unit area in which the combined influence of the various external factors which determine the ecological aspect of the vegetation is such as to produce an essentially uniform environment.* From the standpoint of silvics site may be considered as including everything relating to the factors operating in a geographically definite locality so far as these factors influence forest vegetation. Thus the site is very complex, being the result of the interactions of many varying factors. Although the term is applied to areas in which all the environmental conditions are essentially uniform throughout, it is sometimes used with much broader application (Nichols, 1923).

5. Site Quality

Both the kind and quantity of vegetation produced per unit of area are correlated with site factors. A change in factors causes a change in the volume of wood produced as well as a change in the character of the vegetation. Thus a change in available water supply below the optimum for a given type of vegetation lowers the volume of yield and thus changes the site quality for that type. *Site quality* is a term used by foresters to indicate *the productive capacity of an area of forest land, usually for a given species or a combination of species.*

Although the site factors, in the final analysis, determine site quality it has been the custom in Europe to base site quality on yield obtained in the past or predicted for the future. When the history of a forest is known and records are kept of yield, it is possible to divide the forest into a variable number of site quality classes based on yields actually obtained. In most cases, however, these actual yields for one reason or another do not measure yield capacity — because of defective stocking, insect depredations, and other disturbances from within or without — and without corrections are not a true index of site quality.

Classification of a given site as to quality usually depends on what species or combinations of species that will grow on it constitute the present or prospective stands. Thus a second quality site for white pine may be a first quality site for jack pine. A classification of sites into quality classes irrespective of species is of little value. The classification should be in terms of definite species or combinations of species. The Committee of the Society of American Foresters on the Classifica-

tion of Forest Sites recommended that " the classification of forest sites should be on the basis of the actual mean annual growth in cubic volume at approximately the age of culmination of mean volume growth for typical well-stocked natural stands of the species present or to be grown on each site " (Soc. Amer. Foresters, 1923).

An alternative method consisting of the use of plant indicators of site quality has been developed with conspicuous success in the spruce-pine forests of Finland by Cajander (1926, 1930). He found that certain species of shrubs or herbaceous plants are commonly found growing under the forest canopy on good sites, others on medium sites, and still others on poor sites. This method has also been tried limitedly in the western United States by Korstian (1917, 1919) and in the northern United States and Canada by Ilvessalo (1929), Heimburger (1934), and Sisam (1938). It is quite possible that further use may be made of the subsidiary vegetation in site classification in North America. As yet only in a few forest types have the most useful plant indicators been identified. Unless some method is developed by which a rational numerical evaluation of the site classes is made possible, determinations of tree growth on each forest site will probably still be necessary.

Although either mean annual increment or total yield in cubic feet for a given period of time is the best indicator of site quality, adequate data upon which the assessment can be made are not available for many forest types, suitable well-stocked natural stands are rare, and the field measurements and subsequent computations are time consuming and expensive. Height growth, which can be determined easily and quickly, is an indicator of more practical utility. Height growth is, therefore, in general use in this country as an index of site. Contrary to the argument of Bates (1918) that height growth does not sum up all the qualities of site in which foresters are interested and which they attempt to express in the term site quality, Roth (1916), Frothingham (1918), and others have advocated its use. For a given species variations in height growth due to variations in site factors are closely and positively correlated with changes in volume growth that are similarly caused (Bruce and Schumacher, 1942). The basis for the classification of site quality commonly used under this method is the height in feet of the average dominant tree in the stand at some arbitrarily chosen standard age, usually 50 or 100 years. Often, however, the average height attained by the dominant and codominant trees is used. *The site index for even-aged stands of any species or forest type is usually regarded as the height of the average dominant tree at some standard age, such as* 50 *or* 100 *years.* The younger age is commonly used for

rapidly growing species, particularly in the eastern and southern United States.

The relationship between the site index for loblolly and shortleaf pines and stable physical properties of the soil profile has been evaluated by Coile.[1]

6. Factors of Site (Habitat Factors)

The careful and detailed study of sites has been scarcely begun and it is difficult, if not impossible, to recognize and delimit sites in an absolute sense. Topographic boundaries often may be recognized, but often, though boundaries actually exist, they are not perceived. Sometimes contiguous sites may be sharply delimited, but more often they merge into each other so gradually that a real line of demarcation can not be drawn. All sites agree in the possession of certain essential factors which are termed factors of site and which are universally present. The differences in sites are due to the relative intensities and duration of action of these factors, which are probably not exactly the same for any two.

As the character of a given site is determined by the combined influence of all the conditions in the environment which affect the vegetation, a site factor is any one of these conditions which either directly or indirectly influences the nature of the site. A classification of these factors which restricts their use within precise bounds is practically unattainable. Many classifications have been attempted. The one presented below will serve as a basis for the analysis of the site factors which follows.

The most casual observation will show that the trees and other kinds of vegetation on one site are more or less different from those on another. When we inquire into the reasons for this difference, we find that sites differ not only in the vegetation which they support but also in climate, soil, and in other factors. All these factors cause the differences in the vegetation on different sites. Both silviculturists and ecologists recognize the various factors, to the combined effect of which vegetation is the response, as the factors of site. They may be divided into directly operating and indirectly operating factors. Directly operating factors are those, such as solar radiation, humidity, and soil moisture, which act directly on plant functions and produce a recognizable effect.

[1] T. S. Coile, 1946. Relation of soil characteristics to the site index of loblolly pine and shortleaf pine in the lower Piedmont region of North Carolina. (Unpublished manuscript.)

Thus a decrease in the relative humidity of the air causes an immediate increase in transpiration. Indirectly operating factors are those, such as slope and the flora and fauna of the soil, which affect forest vegetation primarily through their action on the direct factors. Some factors operate with reasonably uniform intensity over large areas, as humidity and atmospheric temperature; others operate with uniform intensity within smaller, more localized limits, as soil composition and soil moisture. These factors which are responsible not only for the ecological characteristics of present vegetation but also for successional changes, may be placed in the following four categories:[1]

1. Climatic factors
2. Edaphic factors
3. Physiographic factors
4. Biotic factors

7. Climatic Factors. — The climatic factors relate to atmospheric conditions and include all factors influencing plant life which are associated with the atmosphere. Possibly with equal justice they may be called atmospheric factors or meteorological factors. Taken as a whole they make the greatest imprint on the vegetation of large areas; however, the extent of their influence may be either regional or local. When regional they refer to conditions delimiting climatic regions; when local they refer to conditions modifying regional climate due primarily to topographic variations and interrelations of land and water bodies within any given climatic region. Although climatic regions and their correlation with regional climatic factors are recognized, these factors are so modified by local conditions that climate is probably not exactly the same at any two places.

There are everywhere both rhythmic and progressive changes in climate. The rhythmic changes are recurrent alterations due to change from day to night and from season to season. Recurrent alterations due to weather cycles may also be placed in this category. The progressive changes are progressive alterations due primarily to increasing or decreasing temperature or aridity occasioned by changes in climate over more or less extended periods of time, as illustrated in progressive climatic changes since the last glacial era. In the main, progressive changes are so slow that the climate of any particular place, in reference to its effect on the vegetation, is essentially stable.

[1] Some writers recognize two additional categories, namely, anthropeic and pyric. The authors have placed the factors listed under these additional categories in the biotic category. They recognize that, in any terminology dealing with such a complex subject as silvics, borderlands occasion divergent opinions.

Atmospheric conditions which determine regional and local climate relate chiefly to temperature, moisture, and light. The factors which determine these are: solar radiation, air temperature, atmospheric humidity, and precipitation. To these four, however, may be added wind, lightning, and atmospheric impurities which operate in the atmosphere and are often of great silvical importance.

8. **Edaphic Factors.** — The edaphic factors relate to soil conditions. Those that directly affect forest vegetation are: soil composition, soil moisture, soil temperature, and soil gases. Their effect is expressed in the differences in forest vegetation on wet soils as compared with dry soils, on sandy soils as compared with clay, on warm soils as compared with cold, and on acid soils as compared with neutral or alkaline.

9. **Physiographic Factors.** — The physiographic factors include the conditions which determine form and structure of the land surface and the rhythmic and progressive changes in these conditions. Those conditions that indirectly affect forest vegetation through their effect on the direct factors are topographic in nature and are earth configuration, altitude, slope, and exposure. Their effect is expressed in the differences in forest vegetation on upper slopes as compared with lower, on northern exposures as compared with southern, and on coastal borders as compared with inland areas.

Rhythmic changes in physiography are expressed in seasonal changes in water level and in the daily rise and fall of the tide in littoral regions. They are of little importance in silviculture. The progressive changes, however, are of vast and far-reaching importance. They are brought about through erosion and deposition and through emergence and subsidence which not only cause changes in topography but also changes in soil conditions. Although changes due to emergence and subsidence take place so slowly that they can usually be estimated only in terms of geological time, changes due to erosion and deposition may be consummated within relatively short periods. Rapid, progressive changes are illustrated in the washing out of deep gulleys, often in a single season, in the building up of flood plains, and in the filling in of swamps and shallow ponds. When progressive changes in topography are rapid, they exercise marked effect on the site and on vegetation. In general, however, when progressive change is not perceived, the topography of any given area may be considered stable.

10. **Biotic Factors.** — The biotic factors relate to conditions that are attributable, either directly or indirectly, to plant and animal agencies. Although the climatic and edaphic factors of site have a predominant influence on forest form and growth, the development of vegetation

under them is arrested, retarded, or more or less completely interrupted or changed, owing to the interactions of plant and animal life, including man. These interactions of various forms of plant and animal life with the trees in a forest are of great importance. It is the duty of foresters to encourage the presence of those forms of life that are directly beneficial to the trees or indirectly beneficial through their effect on the soil. Also foresters should discourage the presence of those forms that are directly destructive, or indirectly so through their action on some other site factor.

11. Classification of Site Factors Based on Their Mode of Affecting Vegetation

Although students of plant life usually classify the factors of site on the basis of their source or origin as presented above, they may be classified, and possibly with better logic, from their mode of affecting vegetation. Thus the preceding classification and the discussion in later chapters place emphasis on the sources of the factors and the analysis of the manner in which they individually affect trees and vegetation. The following classification emphasizes the environmental conditions most potent in determining the character and development of vegetation without reference to their origin (Livingston and Shreve, 1921). These environmental conditions are:

1. Moisture
2. Temperature
3. Light
4. Chemical
5. Mechanical

Although the above classification of environmental conditions is simple and points to the real nature of the factors in their effect on vegetation, it does not stress the sources of the environmental conditions, which are of particular practical importance to foresters. Moisture in relation to plant life without reference to its source is of purely physiological significance, but as soon as it is linked up with its origin, for example, soil moisture, precipitation, and atmospheric humidity, it becomes of ecological significance. Again, temperature without reference to its origin, for example, air temperature, temperature of solar radiation, and soil temperature, is of purely physiological significance. It is the study of the causes of the effective factors, as well as the effective factors themselves, that is of importance in correlating vegetation with its environment.

PART I. ENVIRONMENT OF FORESTS

CHAPTER II

SOLAR RADIATION

1. IMPORTANCE

The chief source of energy for green plants and all life dependent upon them is solar radiation. It is absorbed by plants directly as heat and is also transformed by them into potential chemical energy. Ever since plants first appeared on the earth during the early geological ages, solar radiation has influenced their development. Since green plants are dependent upon light [1] for the synthesis of their food supply, light has long been recognized as one of the major factors influencing growth, development, and reproduction of vegetation.

Foresters base many of their silvicultural practices upon the relative light requirements of forest trees or upon their relative tolerance of shade. Many foresters and plant ecologists have assumed that the arrangement of forest vegetation in vertical layers or zones, from the lesser vegetation on the forest floor to the upper layer forming the overstory, is controlled by intensity, quality, and duration of the light that reaches each layer. Thus the presence or absence of tree reproduction, shrubs, and herbaceous plants beneath forest canopies has been generally attributed to light conditions. The presence of certain species and the absence of others frequently have been explained by their relative, inherent capacities for survival and growth under different degrees of shading.

2. RADIANT HEAT AND LIGHT

The radiant energy of the sun reaches the earth's surface as electromagnetic waves of varying lengths (Fig. 1). Among the important phenomena of sunlight are reflection, refraction, interference, polarization, and dispersion. If a beam of sunlight is passed through a suitable prism, the beam which enters as white light is dispersed into red, orange, yellow, green, blue, and violet lights, although each color merges by insensible gradations into the next. This band of intergrading colors

[1] The term "light" is often used loosely as being synonymous with the solar radiation received at the earth's surface, instead of in the stricter sense as referring to that part of the spectrum which is visible to the human eye.

is known as the visible spectrum (Fig. 2). The wave length of the violet ends at about 400 mμ. (millimicrons) and the red terminates at 720 mμ. This portion of the radiant energy to which the human eye is sensitive is known as light. Although the eye is not sensitive to wave lengths much longer than 720 mμ. or shorter than 400 mμ., other means have proved that the wave lengths of solar energy extend

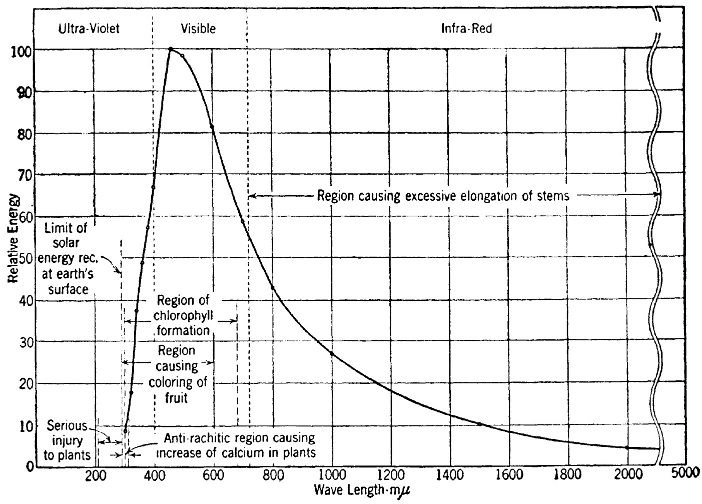


FIG. 1. — Distribution of energy in the ultra-violet, visible, and infra-red regions of the solar spectrum at the earth's surface *(From Fowle, 1933)*. Regions causing various biological effects are also indicated *(Mostly from Duggar et al., 1936)*.

on either side of the visible spectrum. Energy composed of wave lengths longer than 720 mμ. is known as the infra-red, and that shorter than 400 mμ. as the ultra-violet. The solar radiation received at the earth's surface lies almost entirely between wave lengths of 290 mμ. and 5,300 mμ. (Abbott, 1929).

The maximum energy of solar radiation occurs in the green and yellow parts of the spectrum. About 1 percent of all the sun's energy reaching the earth is ultra-violet and about 60 percent is infra-red. The visible spectrum, therefore, contains somewhat less than one-half the total radiant energy received from the sun.

Although the physical, chemical, and biological effects of solar radiation vary markedly with wave length, one effect occurs at uniform intensity throughout, namely that of heat. Consequently the heat

energy of solar radiation may be used in measuring the radiation intensity regardless of wave length.

3. Solar Radiation that Reaches Earth's Surface

The sun itself is not a constant source of light. Variation may occur in the amount of energy emitted due to sun spots which appar-

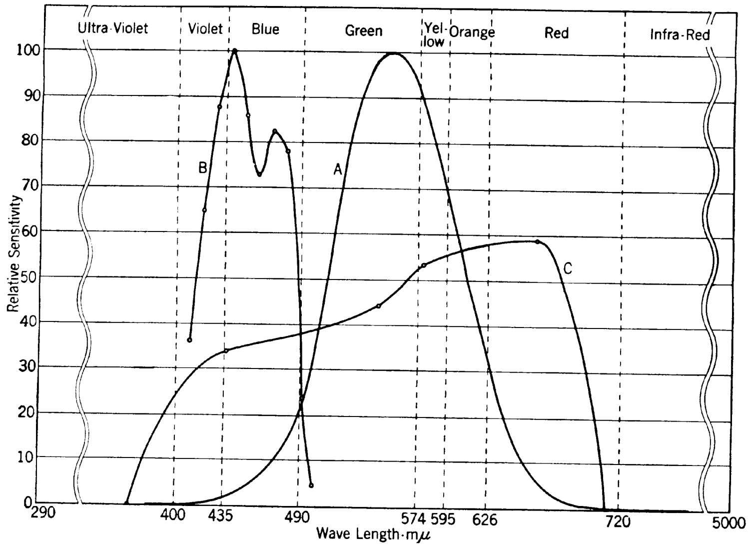


FIG. 2. — Certain biological effects of radiation in the different regions of the solar spectrum: *A*. Relative visibility to the human eye (*After Brackett, 1936*); *B*. Relative effect on phototropism (*After Johnston, 1934*); *C*. Relative effect on photosynthesis (*After Warburg and Negelein, 1923*).

ently have an important influence on climate (Abbot, 1936). Both the intensity and quality of the solar radiation that reaches the earth's surface varies with latitude, altitude, season of the year, and time of day (Kimball, 1936). The solar radiation reaching the surface of the earth may be still further modified by local obstructions due to topographic features and vegetation and by atmospheric conditions resulting in scattering and absorption. The degree of absorption of solar energy by the atmosphere depends upon the pressure and quality of atmospheric gases. The least transmission occurs when the pressure is greatest. The losses from incoming solar energy are due mainly to scattering

and selective absorption by water vapor and permanent gases in the atmosphere, to absorption and reflection by clouds and dust particles in the air, and to absorption in chemical reactions (Pulling, 1919).

The solar energy which reaches the vegetation growing on the earth's surface is chiefly altered by the earth's atmosphere. Solar radiant energy passing through dry air is only slightly absorbed, but clouds heavily laden with moisture may screen out 99 percent of the light or more. The total light received during any given day may be only 3 to 5 percent of that received on the following day in regions where storms are followed by exceptionally clear days. Clouds not only greatly decrease the quantity of light but also change its quality by absorbing the longer wave lengths to a greater extent than the shorter ones. The scattering of the energy of short waves compensates for the absorption of long ones to some extent, so that the actual change is not so great except for passing clouds on an otherwise clear day.

4. EFFECTS OF SOLAR RADIATION ON FOREST VEGETATION

Solar radiation is known only by its effects. These effects may be divided into four groups: (1) heating, (2) illumination, (3) chemical, (4) electrical. The heating and chemical effects of solar radiation are most important to plants, because of certain physiological responses in trees and other plants, responses due apparently to the heating and chemical effects of solar radiation and to the duration of their effectiveness. Photosynthesis and certain other important responses of plants belong to the group of chemical effects which depend upon radiation within the visible region or " light."

5. Effects of Light

A large amount of the radiant energy absorbed by plants becomes effective as heat, which vaporizes water in the cells and intercellular spaces. This vaporization tends to increase the loss of water from the cells.

In leaves grown in strong sunlight many of the chloroplasts lie in line with the light rays, thus screening each other from the full effect of the radiant energy. In shade leaves they are arranged at right angles to the light rays increasing the surface available for absorption (Weaver and Clements, 1929). Of all the plant organs leaves undergo the greatest change in response to light. The formation of palisade cells at right angles to the leaf surface is a common result of continued exposure of leaves to sunlight. The amount of palisade tissue de-

veloped in the same plant may vary greatly. The leaves in the upper part of a tree crown fully exposed to the sun are very different from those in the shaded interior of the crown.

Light is the most important environmental factor modifying the daily opening and closing of stomata (Weaver and Clements, 1929). Light is also known to cause the turning of stems and leaves and the assumption of day and night positions of leaves. Stems may be modified considerably because they usually contain chloroplasts and bear the leaves.

Light affects the form and structure of plants and profoundly influences certain physiological functions. The primary response of trees to light is the production of chlorophyll in the leaves. Light is necessary for the synthesis of carbohydrates from carbon dioxide and water by all green plants. The physiological significance of this process, known as photosynthesis, lies in the fact that it involves a transformation of the radiant energy from the sun into chemical energy (Stiles, 1925; Spoehr, 1926; Spoehr and Smith, 1936).

The effects of both the quality and intensity of light and also the effects of intermittent light on the rate of photosynthesis have received considerable study. The quality of light is determined by its spectral energy distribution — the distribution of the energy received over the different parts of the spectrum — and the light intensity is the amount of energy falling on a unit surface in unit time.

6. Light Intensity and Photosynthesis. — Foresters are interested chiefly in the effect of the environment upon photosynthesis rather than in the dynamics or biochemistry of the process. Therefore, it is of special interest to know the course of assimilation of carbon dioxide in leaves attached to trees functioning under varying environmental conditions, and consequently subjected to the influences of the constantly changing external and internal factors which may affect not only photosynthesis but also all other metabolic processes (Heinicke and Hoffman, 1933). Variations in the intensity of light and heat derived from solar radiation have a very pronounced effect upon the photosynthesis of leaves under natural conditions.[1]

Photosynthesis occurs, when other factors are not more significant, under the entire range of the visible spectrum (Fig. 2) and under a wide range of light intensity. When the light intensity is too low, photosynthesis is inadequate to replace the loss of energy due to respiration; when it is too high, the stomata close, the closing of which may in turn

[1] The extensive literature on the effect of light on photosynthesis has been reviewed by Spoehr and Smith (1936).

depress the rate of photosynthesis. The daily rate of both respiration and photosynthesis tends to follow in general the extent of opening of the stomata (Johannson, 1926). The falling off in the accumulation of dry matter at high light intensities is due to the effect of stomatal openings in reducing the free interchange of gases between the atmosphere and the interior of the leaf and the consequent reduction of CO_2 available for photosynthesis.

Trees accumulate potential energy in the formation of new organic substances by the process of photosynthesis. They release energy through the oxidation of carbon compounds, that is, through respiration. When light intensity is above the minimum necessary for a tree, the building up of organic material goes on faster than the breaking down. When light intensity falls below the minimum requirements and remains there, the tree soon ceases to grow, owing to the lack of carbon accumulation, and finally dies.

It is generally accepted that with low light intensities, such as occur under the densest forest canopies, the rate of photosynthesis is proportional to the light intensity. Enough light is usually present, even under very dense forest canopies, for photosynthesis to occur, although its rate will depend upon the intensity of light. However, under very dense canopies the light intensity may be too low for photosynthesis to balance respiration. As the light intensity increases, the rate of photosynthesis is no longer proportional but tends to approach a constant value with many species long before full light intensity is reached, unless other factors affecting photosynthesis also are increased.

In the earlier studies on the minimum light requirements of trees, attempts were made to measure light intensity at points in the forest where leaves and branches were dying and where reproduction was failing. It was assumed that the death of branches in the interior of crowns and the failure of seedlings on the forest floor were due to low light intensity and change in light quality. It appears, however, from more recent studies that sometimes these failures may be due to a complex of factors rather than low light intensity alone. (See Chapter X.) More recent researches show that the forest plants studied are able to utilize CO_2 and form carbohydrates faster than they are consumed in respiration, under remarkably low light intensities provided other factors are favorable.

Only a relatively small percentage of the solar radiation is utilized by plants in photosynthesis. Brown and Escombe (1905), from many experiments conducted under a wide range of light intensities, conclude that the proportion of energy used in photosynthesis averages about

1 percent. Recent calculations for pine forests in Wisconsin by Shirley (1936) give even lower values. When the light is less than about 15 percent of full sunlight, Heinicke and Hoffman (1933) found that maximum assimilation cannot be expected with apple leaves. In later work with an entire apple tree, Heinicke (1935) found that respiration exceeded photosynthesis from the time the leaves opened until petals fell. After that there was a gradual increase in apparent photosynthesis until about the latter part of June when most of the leaf surface had been formed. A rapid decline in photosynthetic activity occurred after the first heavy frost when many of the leaves began to drop. He found wide fluctuations in the apparent photosynthesis from day to day and during different periods on the same day, depending primarily upon the light intensity and the widely variable CO_2 content of the air. When the entire tree is considered, light is undoubtedly a very significant factor, for a large part of the leaf surface lies in the interior of the tree crown where, on all except the relatively few intensely bright, clear days, they received inadequate light for maximum photosynthesis.

Working with potted seedling trees, Burns (1923) placed a number of species in a controlled atmosphere where all factors of the site except light intensity were at or near their optimum for growth. By varying the intensity of light, the minimum intensity required to balance the carbon dioxide used in photosynthesis with the amount liberated in respiration was determined. A loss of CO_2 from the controlled atmosphere at the end of the experiment was an index of the increase in the organic matter in the plant due to photosynthetic activity. A gain in CO_2 was an index of the consumption of stored organic matter in the plant and a consequent decrease in dry weight of the plant. Based on the minimum light intensity at which the CO_2 produced by respiration equaled that consumed in photosynthesis, the species studied by Burns may be arranged in the relative order of their minimum light requirement from the lowest to the highest as follows: *Acer saccharum, Fagus grandifolia, Tsuga canadensis, Picea excelsa, Pinus strobus, Picea engelmannii, Celtis occidentalis, Quercus borealis, Pinus contorta, Pseudotsuga taxifolia, Larix laricina, Thuja occidentalis, Pinus sylvestris*, and *Pinus ponderosa*.

Using artificial light and measuring the energy of radiation with a Coblentz thermopile, Bates and Roeser (1928) compared various coniferous seedlings grown for 9 months under a considerable range of light intensities. The following data, calculated from their experiments,

show the theoretical minimum light in percentage of full light in which growth could be made in the several species:

	PERCENTAGE
Sequoia sempervirens	0.62
Picea engelmannii	1.10
Pseudotsuga taxifolia (Wash.)	1.30
Pseudotsuga taxifolia (Colo.)	1.50
Pinus ponderosa (Colo.)	1.80
Pinus ponderosa (Ariz.)	1.80
Pinus strobus	2.00
Pinus banksiana	2.38
Pinus contorta	2.40
Pinus resinosa	2.55
Pinus flexilis	2.70
Pinus edulis	6.30

Grasovsky (1929) grew various conifer and hardwood seedlings under conditions favorable for them but varied the light intensity in order to determine the critical points at which vigor and survival were no longer possible. His experiments were conducted in sunlight and the intensity was measured with a Macbeth illuminometer, which measures the visible spectrum. Three-year-old potted plants of several species were grown in four series, under conditions favorable for growth but with each series exposed to different light intensities. In one series the maximum illumination was 10,000 foot-candles and in the other three 300, 65, and 25 foot-candles, respectively. At the end of 10 months all plants exposed to a maximum of 300 foot-candles or more were in a vigorous or good condition and showed growth. Those exposed to a maximum of 65 foot-candles varied from good to dead, and those exposed to a maximum of 25 foot-candles were, with one exception, dead. These experiments indicate that at least some trees can live and show new growth over a period of 10 months under a sunlight intensity never higher than 300 foot-candles or between 3 and 4 percent of the maximum light intensity in the open.

The work of these and other investigators shows that the light intensity required for a carbon dioxide balance — that is, when the carbon dioxide given off in respiration will just be used up in photosynthesis — is only about 1 to 5 percent of full sunlight. Plants are found under natural forest canopies where the light intensity is below 5 percent, but Daxer (1934) has observed that, in many of these plants,

photosynthesis exceeds respiration only in the spring before the leaves of the overstory are fully developed.

Several research workers, after determining the minimum light intensity required for the survival of each species studied in a controlled environment, measured light intensity under natural stands in various types of forest. They used the same methods for measuring light employed by them in their earlier experiments. They compared the light intensities under stands with the minimum light under which the plants were able to survive in their experiments. They found that light intensities under natural, closed forest canopies are usually below 25 percent and may vary from 0.16 to 35 percent. However, values as low as 2 percent are not uncommon in hardwood or dense conifer forests. The weight of experimental evidence clearly shows that the minimum light intensity required for photosynthesis to balance respiration is very low as compared with full light in the open, occasionally less than 1 percent. Redwood, which Bates and Roeser (1928) report as having a minimum light requirement of less than 0.7 percent and capable of increasing its original size almost ten times in light of 10 percent intensity, stands out as having the most efficient photosynthesis of the forest-tree species studied. They found that Douglas fir and Engelmann spruce seedlings increased in dry weight under a light intensity of from 1.1 to 1.5 percent of full light in the open. They state that light intensity is not likely to be so low in ordinary forests as to prevent seedling survival.

Shirley (1929) concluded that the light needed for the survival of the plants grown in his experiments is very low, being less than 40 foot-candles for all except the sunflower, which requires a much higher intensity. Redwood and loblolly pine were able to survive for 6 months under a light intensity at which they were barely able to increase in dry weight, but sunflowers died within 2 or 3 weeks. At low light intensities he found that the dry weight produced by his experimental plants was almost directly proportional to the intensity received up to about 20 percent of full summer sunlight. He also found that chlorophyll concentration increased with decreasing light intensity until the intensity was so low that it hazarded survival. Further decrease in light intensity caused a decrease in chlorophyll concentration.

Light is not a direct factor in initial seedling mortality of western white pine and associated species in northern Idaho (Haig, 1936). Seedlings are able to survive the first season or even longer under intensities as low as 5 percent of full sunlight if not killed by biotic agents or drought; but light may be an important direct factor in survival through its effect on growth, particularly on initial root penetration.

Actual failure to synthesize food materials and produce some growth is not considered to be as critical for seedlings as certain other conditions. For example, slow growth, and especially an insufficient nutrient supply for the roots, results in seedlings improperly developed to withstand such desiccation of the surface soil as often occurs late in the normal growing season.

7. Light Intensity and Growth. — Growth, as determined by increase in dry weight, is dependent upon the total product of photosynthesis minus that portion used in respiration. Therefore, light, through its effect on photosynthesis, has a significant effect on growth.

In the morning and evening maximum photosynthesis occurs in full sunlight. During mid-day, however, high light intensity causes an increase in leaf temperature with a consequent desiccating effect (Curtis, 1936). This may cause closing of the stomata and reduction of photosynthesis. Likewise in cloudy weather full sunlight gives maximum growth and maximum photosynthesis. Consequently, it is presumptuous to state that any definite percentage of light is optimum for growth. If all other factors could be accurately maintained at the optimum, then full sunlight would result in optimum growth, but because this is rarely so in forests some reduction in light intensity — for example to one-half — might not materially reduce growth. The development of tissue involved in the growth of green plants beyond the juvenile stage depends upon the amount of carbohydrates produced less that used in respiration.

The effects of light upon plant growth have been studied by a number of workers with fairly definite results. The amount of dry matter produced usually increases with increasing light intensity up to a certain maximum and then decreases (Lubimenko, 1908). The optimum intensity for growth varies with temperature and the concentration of chlorophyll. Chlorophyll formation depends upon light intensity, but the optimum intensity for its formation is below that for the optimum production of dry matter. The accumulation of dry matter is proportional to total photosynthesis (Heinicke and Hoffman, 1933).

Extremely high light intensities favor root growth more than shoot growth (Shirley, 1936). They also cause excessive transpiration in plants, which results in short stems, thicker but smaller leaves, increased water-conducting tissues, and reduced growth. High light intensities tend to increase the alkalinity of the cell sap. In extreme cases this may interfere with the iron nutrition of plants, causing them to become chlorotic through the breakdown of chlorophyll. At extremely low light intensities nutrition limits the development of leaves and re-

stricts growth, even though the large, thin leaves, high in chlorophyll content and widely spaced on the stem, provide very efficiently for photosynthesis. Flower and fruit production does not occur in very weak light, but takes place at moderate intensities. Deficient light may delay the time of flowering and fruiting (Zillich, 1926). The light intensity for optimum development of flowers and fruit, as well as for the maximum production of dry matter, is higher than that required for the best vegetative development (Shirley, 1936).

The most vigorous vegetative growth occurs at moderate light intensities whenever ample food (carbohydrates and proteins) is available (Shantz, 1913). However, since this food is dependent upon total photosynthesis maximum growth is often attained in full intensity of sunlight (Rosé, 1913; Garner and Allard, 1920). The percentage of dry matter in tops, ratio of dry weight of roots to dry weight of shoots, density of growth, strength of stem, and leaf thickness all increase with increasing light intensity (Shirley, 1929). Height growth decreases with increasing light when the light values are high, but at lower intensities height growth increases with light.

Light intensity frequently has a marked effect on the survival and growth of forest-tree reproduction. The survival of Norway and northern white pines and white and red spruces in prepared seed spots was poor for all species in the shade in the four forest types of Mount Desert Island, Maine, studied by Moore (1926), except in the northern hardwood type. The growth and vigor of the seedlings were in every case markedly better in the small openings. Gast (1930), in correlating continuously recorded measurements of total solar radiation (Fig. 3) with measurements of leader growth of northern white pine at three different stations where cuttings had been made in the forest, found that the leader growth of this species is apparently directly proportional to the radiation, up to the intensity of full sunlight. He concludes that, for white pine in New England, the minimum radiation intensity necessary to maintain photosynthesis and survival of reproduction fails to provide for adequate transformation of humus with a consequent lack of nitrogen. The great fluctuations in the light intensity at a given point under a living canopy are due to flecks of sunlight that penetrate the forest canopy. Any given point beneath the canopy is subject at intervals to relatively high light intensity and at others to relatively low.

After a good seed year of ponderosa pine in the southwestern United States, Pearson (1929, 1930) found that seedlings of this species would come up even more abundantly on bare areas under the clumps of trees

than in the openings, although practically all of those in dense shade died or became unthrifty within 4 or 5 years. When ponderosa pine was grown under lath shades in a nursery, Pearson (1936) found that all seedlings in the intensity of approximately 10 percent of full sunlight died during the first winter. All but two of those in 20 percent light died during the 5-year period of the experiment and the survivors

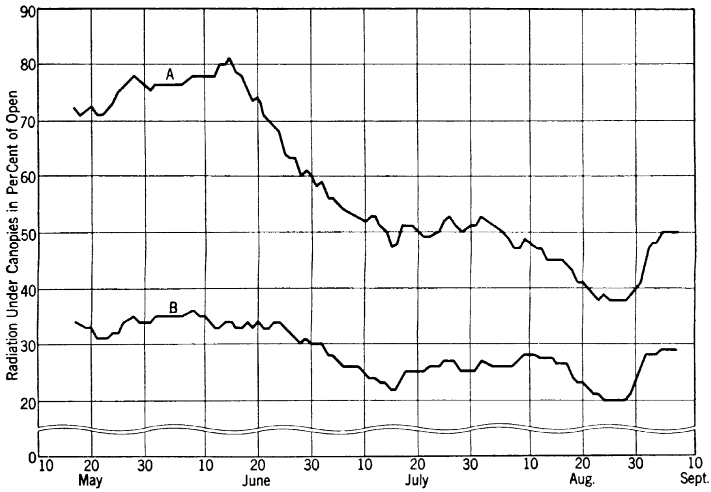


FIG. 3. — Radiation under forest canopies in percentage of that in the open for 1925, plotted as moving 10-day averages of continuous records: *A*. Under a white pine canopy obscuring 40 percent of the sky; *B*. Under 85 percent shade—nearly maximum density for pure white pine stands. (*After Gast, 1930.*)

were much smaller and more slender than those in full sunlight or half shade. The plants in half shade made slightly less height growth but only about half the diameter growth of those in full sunlight.

The intensity of the light reaching the forest floor is usually not so low as to preclude the possibilities of reproduction in fully stocked forest stands. However, light intensity is usually a significant factor in the growth of vegetation under forest canopies. Although the light intensity under such canopies may be adequate for the survival of some plants, it is frequently too low for the establishment of tree reproduction of certain species and is generally too low for the best growth and development of reproduction (Shirley, 1929, 1932). Seedlings appear under quite dense canopies and may persist for from 1 to 20 years or longer; but, if they do not grow at a reasonable rate, they become

victims of one or more of the natural adversities of the habitat and eventually succumb. When the growth of stands is considered instead of the growth of individual trees, or even individual species in mixed stands, a more definite correlation is found between light intensity and height growth.

8. Changes in Light Quality in Forests. — The light incident on a tree growing in the open is to the highest degree unfiltered light, but

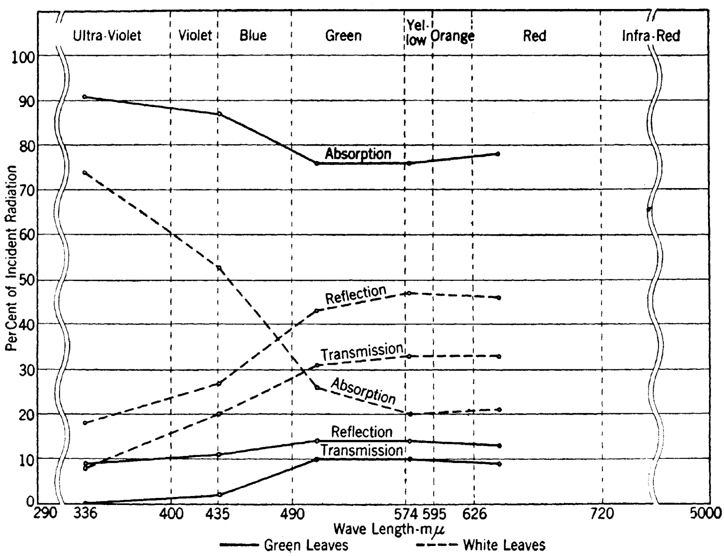


Fig. 4. — Relative transmission, reflection, and absorption of light in the different spectral regions in percentage of the incident light, for green and white leaves of 10 species of plants. (*From Seybold, 1932-1934.*)

a tree growing under a canopy is exposed to an increased percentage of reflected and transmitted light, depending on density of the canopy. The light available for reproduction and other vegetation beneath canopies is of a different quality from that which reaches a tree in the open (Zederbauer, 1907). It is changed in quality in passing through the leaves and by reflection from plant surfaces. Light transmission decreases and absorption increases with decreasing wave length (Seybold, 1932–1934). Absorption is greater throughout in the green than in the white portions of leaves, but it increases more markedly with decreasing wave length in the white than in the green portions

(Fig. 4.) The presence of chlorophyll is obviously responsible for the greater absorption in the green portions.

Light under hardwood forest canopies as compared with zenith skylight is generally very poor in blue, relatively rich in yellow and green, close to sunlight in its content of orange-red, and very much richer than either skylight, daylight, or sunlight in the deep red (Knuchel, 1914; Atkins and Poole, 1931; Atkins, Poole, and Stanbury, 1937). This is probably due to transparency of chlorophyll to the red. According to Knuchel (1914) no significant changes in quality occur under coniferous trees. He measured the spectral transmission of leaves and found them to transmit more yellow and green than red and blue, often transmitting 20 percent in the yellow and green and less in other portions of the spectrum. The intensity of light which passes through leaves exposed to full light is so small that it plays a very insignificant rôle; it varies from about 0.008 to 0.0003 of the total light which reaches them (Griffon, 1900; Linsbauer, 1901; Knuchel, 1914).

Studies made by the senior author at New Haven, Connecticut, on the transmission of light by oak, beech, and other hardwood species gave a greater transmission in early spring when the leaves were young than in late summer. Even late in autumn, after chlorophyll had left the leaves, the transmission was less than in spring soon after the leaves expanded. Therefore it appears that light which passes through the leaves, although changed in quality, can have but little effect on the quality of light on the forest floor. It appears that whatever change in quality there is in the light on the forest floor is due primarily to the quality of the light reflected from leaves and other plant surfaces.

The greatest percentage of light reflected from green leaves usually falls between wave lengths of 500 mμ. and 575 mμ. (Shull, 1928, 1929; Seybold, 1932–1934). In autumn-colored foliage, however, such as the crimson leaves of *Psedera quinquefolia* and the bright yellow leaves of *Betula alba*, the greater reflection falls in the wave lengths between 640 mμ. and 680 mμ. The work of Brown and Escombe (1905) accounts for all the energy inflow in terms of work and transmission, but assumes that the reflection of light from the plant surface is very little. Shull found that the percentage of 90° reflection of bright diffused light from the surfaces of leaves may, in some species and at certain seasons, account for as much as 50 percent of the light incident upon them, as from the lower surface of the leaves of *Populus alba*. In other species, as in the upper surface of the leaves of *Syringa vulgaris*, it accounts for but 3 to 6.5 percent. As the various wave lengths are absorbed or re-

flected in different degrees, the depth of shade and color, as they appear to the eye, vary widely in different plant surfaces. Thus, the dark shade and deep green color of the foliage of *Tsuga canadensis* and *Taxus canadensis* indicate that only a small percentage of the incident light is reflected, and that mostly in the wave lengths corresponding with green. On the other hand, the light shade and the light yellow-green color of the foliage of *Betula populifolia* indicate that a large percentage of the incident light is reflected, and that largely in wave lengths corresponding with yellow. Because of these differences in reflected light, hemlock and yew may absorb more light than gray birch when subjected to equal illumination. When light under canopies becomes so reduced that light intensity is the most significant factor, the first species to disappear are those in which a large percentage of the incident light is reflected from their surfaces. Those which persist at the lowest intensities where other factors are not more significant are the species that reflect a low percentage of the incident light. Species able to survive and even grow under very dense living canopies, such as *Taxus canadensis, Tsuga canadensis, Picea alba,* and *Abies balsamea,* have foliage dark in shade and deep green in color. Species not able to survive under living cover of like density, such as *Betula populifolia, Populus tremuloides, Acer saccharinum,* and *Prunus pennsylvanicum,* have foliage light in shade and light yellow-green in color. The ability of the former group of species to grow better under dense canopies is due in part to the fact that much less of the incident light is reflected from the foliage. However, many species tend to produce darker green leaves in the shade. Depth of hue is also dependent upon thickness of leaf. Thin leaves have the advantage in shade because light can reach a greater proportion of chloroplasts in thin leaves than in thick leaves.

Although the filtered light on the forest floor is changed in quality in penetrating the canopy, this change has but little effect on the rate of growth in reproduction and other vegetation on the forest floor, provided the intensity is sufficiently high (Grasovsky, 1929). Burns (1933) found that infra-red radiation of wave lengths longer than 1100 mμ. is detrimental to photosynthesis. He reports that with Norway and Englemann spruces the relative quantum yields in photosynthesis indicative of photosynthetic efficiency in the wave lengths 720 to 630, 720 to 560, and 470 to 390 mμ, are 9.5, 10, and 5; and with white pine, 9.5, 11, and 5. Later studies of the limits of photosynthesis in white pine and Norway spruce by Burns (1935) showed that these species are able to use all of the visible spectrum, with the exception of part of the

blue and all of the violet. Better growth occurs in the yellow-green region than in the red and blue for equal intensities (Arthur, 1935). The blue portion is more efficient than the red, although it produces plants smaller in size than those grown in normal sunlight (Shirley, 1929). However, the entire visible solar spectrum is more efficient for the growth of plants than any region of it. Although the entire visible spectrum is effective in producing photosynthesis, a maximum rate occurs at about wave length 655 mμ. in the red region and a secondary maximum at about 440 mμ. in the blue (Hoover, 1937).

From the available evidence it appears that under coniferous canopies modification of light quality is insignificant, and that, although hardwood canopies cause a slight increase in the relative amount of green light, this change is of little consequence in modifying the growth of the under-vegetation. The important factor is reduced intensity of light.

9. Light and the Form and Development of Trees. — Quite aside and distinct from the effect of light on the photosynthetic process is its effect on the form and structure of trees and other plants. This effect arises from:

1. The effect of light in preventing etiolation of trees.
2. The phototropic effect of light on trees.

10. Relation of Light Intensity and Light Quality to Development of Tree Organs. — The elongation of the growing axes of trees in the forest occurs chiefly between sunset and sunrise. It is very significant that low light intensities and infra-red radiation tend to stimulate height growth and that white light of high intensity tends to stimulate root growth. Blue light tends to prevent an etiolated form of growth. There is some evidence to indicate that the blue-violet end of the spectrum checks stem elongation (Popp and Brown, 1936). The short-wave ultra-violet rays from the solar spectrum impart slight antirachitic value to certain food plants and irradiation from a quartz mercury vapor lamp during periods of cloudy weather, or when plants are artificially shaded in clear weather, produces an increase in ash and an increase in calcium or phosphorus, or both (Lodjkin, 1931; Stewart and Arthur, 1934).

Arthur (1936) has shown that the excessive stem elongation associated with plants grown under artificial light or under red filters is due to the near infra-red and that it can be held in check by the addition of red light. The near infra-red appears to be of no value and perhaps is harmful, unless it does counteract an apparent "dwarfing" effect.

Trees growing in stands or in openings in stands are subjected to a much lower average light intensity over the entire day than trees in the open. The effect of intensity of illumination is expressed in the size and structure of leaves. The leaves of a given species are smallest when exposed to full light intensity; thus the leaves of oak are smallest at the top of a tree where exposed to full overhead light, and are largest on the lower limbs where shade is deepest. The depth of shade of the foliage is affected by the intensity of the illumination to which a given tree is exposed; trees exposed to deep shade have darker foliage. When plants are grown in very weak light, the leaves are very thin and have only one layer of weakly developed palisade cells and a more or less loosely arranged parenchyma (Korstian, 1925; Shirley, 1929, 1936). When the light is increased moderately the leaves attain maximum size, tend to become more compact, have from one to two well-developed layers of palisade tissue, and develop typical spongy parenchyma. Intense illumination may still further increase the thickness of the palisade tissue.

Very intense light acts fatally on protoplasm. This action is independent of heat. The death of trees, however, from exposure to excessive intensities of light apparently does not occur in nature. The many devices developed in plants which decrease the intensity of the light that reaches the chloroplasts is considered to be an adaptive trait providing protection against injurious intensities. However, it is difficult to differentiate clearly between the responses to excessive light and those to high transpiration. In many trees these responses are shown in the position of the leaves in relation to light, in a coating of hairs, in reflecting surfaces, and in the curling or rolling of leaves.

Leaves and plants grown in full sunlight should be considered normal. Those developed in the shade have an increased leaf surface which tends to compensate for low light intensity. In low light intensities of normal daily length, plants present an etiolated appearance, that is, they show long internodes, weak, succulent stems, vegetative growth only, poor root development, and thin leaves with loosely arranged, thin-walled cells (Shirley, 1936). Thus elongation of stems occurring in the shade is at the expense of sturdiness and, unless the plant reaches full sunlight, a weak individual is developed. In any case height growth in the shade is limited by the food supply. Without adequate light plants suffer malnutrition and ultimate starvation.

It has been generally assumed that, within a given species, the form of crown is largely controlled by light and that the difference in typical form of crown in the open and that in dense stands is due to differences

in the light intensities to which they are exposed. Trees growing in dense stands do not retain their lower limbs in live condition. A variable length of time after death, the limbs decay and fall from the trees, leaving the boles clean, for one-half, often to two-thirds their total height. This dying of lower limbs in stands has usually been considered as resulting from the reduced light intensity which reaches the lower part of the crowns, although it has not been definitely demonstrated. Pine leaves persist longer on the north side of the crown although the light is less (Stålfelt, 1921). There is apparently a correlation between available light and failure of spruce buds to open (Stålfelt, 1931).

11. Relation of Light Intensity and Light Quality to Phototropic Effects. — The effect of light on the form of trees is strikingly expressed in phototropism. Most chlorophyll-bearing plants bend toward the source of light. Thus a tree growing beneath the spreading branches of another bends outward or away from the axis of the larger tree. This phototropic response is explained by Strasburger (1930) and others as being the result of the checking of elongation on the side of a plant toward the source of light while the side away from the light continues to elongate. When the tree or other plant is equally illuminated on all sides it does not bend, no matter how low the light intensity. The infra-red is the only region which appears actually to stimulate elongation (Arthur, 1936). The blue-violet region appears more efficient in overcoming excessive elongation, but may also produce the same results. Johnston (1934, 1936) has very carefully worked out the relation of phototropism to wave length (Fig. 2). As the phototropic movements are responsible in part for the form of a tree, the blue-violet region of the visible spectrum performs a special function in this respect.

Phototropism has been regarded by Engler (1924) and Cieslar (1923) as responsible for crooked stems in many trees. Some species, such as spruce, appear to be immune to phototropic responses and grow straight regardless of local light differences, whereas many hardwoods, particularly oak and beech, are quite susceptible. On this basis they advise conifer-hardwood mixtures.

12. Influence of Light Intensity on Winter Hardiness and Drought Resistance. — Resistance to cold and drought as well as to disease, insect attack, and other unfavorable influences is improved by good light conditions, that is, light conditions which favor the maintenance of a carbohydrate reserve. Light has a profound influence on the hardening of plants against cold (Dexter, 1933). Continuous cold in

light or cold nights and warm days both induce hardening, but cold days and warm nights or continuous cold in darkness do not. Any treatment involving low temperature which tends to favor photosynthesis and retard respiration and growth aids hardening. Hardiness is decreased by shading (Auchter and Schrader, 1929). Plants developed in the shade are less resistant to drought than those grown in full sunlight.

13. Duration of Radiation and Effects

Owing to altitudinal and latitudinal differences the relative proportion of daylight to darkness over a period of time varies greatly in one place as compared with another. Length of day through its influence on flowering, fruiting, and dormancy has a very important effect on the distribution of plants. Also, when the radiant energy available to plants is distributed over a longer period of time at a lower intensity than when the opposite condition holds, they may function more efficiently from the viewpoint of tissue production (Davis and Hoagland, 1928). Garner and Allard (1920, 1923, 1931) experimented on a number of plant species in which the normal number of hours of exposure to sunlight was shortened to a varying extent by moving the plants into a dark chamber a part of each day. Besides many species of herbaceous plants, they experimented with several species of woody plants, including apple, yellow poplar, boxelder, winged sumac, and smooth sumac. They report that yellow poplar, given daylight supplemented by electric light until midnight, grew all winter, while smooth sumac treated in the same manner retained its leaves during the winter but made no growth. In winged sumac leaf fall was retarded only a few weeks by this treatment. Apple made more growth with 10-hour days than with the normally long 14- or 15-hour days of midsummer, but boxelder grew better with the long summer days. From these experiments they concluded that the length of day might be an important factor in determining the time both of beginning and of ending the dormant period. From their experiments on the effect of the photoperiod in initiating or suppressing sexual reproduction in herbaceous flowering plants they concluded that some plants are more sensitive than others to length of day. Some of the more sensitive species are caused to flower more quickly with long days, others with short days.

Kramer (1936) observed the behavior of potted seedlings of white ash, green ash, beech, yellow poplar, black locust, red gum, post oak, northern red oak, white oak, and loblolly pine under various lengths of day. He found that with the normal length of day in central North

Carolina all of these species ceased growth as early in the autumn in a warm greenhouse as out-of-doors, although most species did not lose their leaves as soon indoors. All species except red oak and white and green ash made more growth and grew later in the autumn when daylight was supplemented by electric light to give a total period of illumination of 14.5 hours. Several species were grown with an 8.5-hour day and most of these made less growth and became dormant sooner than with normal day. With a 14.5-hour day, loblolly pine grew all winter, but made better growth with continuous light. A 16-hour day caused red gum and yellow poplar to grow practically all winter. The resumption of growth in dormant beech, yellow poplar, red gum, and red oak was hastened by additional light and retarded by shortening the photoperiod below the normal length of day.

Available evidence indicates that periodicity of growth in many woody plants native to temperate zones does not depend so much on the periodicity of temperatures favorable to growth as upon the length of day. In other words, it appears that the duration of the growing season for certain species is, to a considerable extent, controlled by seasonal variations in length of day. These results also strongly uphold the view that dormancy is not the result of an inherent rhythm in plants, but of the action of various environmental factors. From observations on herbaceous flowering plants it is evident that not only growth but also the time required for reaching and completing the flowering and fruiting stages are profoundly affected by variations in length of daily exposure to light.

14. Temperature Effects

Each particular species must have an environment which provides temperature extremes falling between certain, though ill-defined, limits. The tree receives its required heat from (*a*) absorption from the atmosphere, and (*b*) direct solar radiation.

Temperature data from thermometers and thermographs protected from the sun's rays are not adequate to determine the heat requirements of trees or the heat characteristics of sites. In order to ascertain the effective temperature, it is necessary to determine not only the air temperature but also the thermal energy of solar radiation.

The thermal energy of radiation may be effective through soil temperature as well as air temperature. Transpiration increases with increase in soil temperature (Clements and Martin, 1934). This favors more rapid photosynthesis which cannot occur without rapid transpiration in full sunlight.

A species growing in the colder portions of its range or in the Arctic

requires exposure to more direct solar radiation than when growing in warmer localities. The deficiency in air temperature and lower light intensity must be compensated for by growing the species in more open stands, which admit more direct solar radiation and consequently are subjected to higher soil temperatures than obtain in dense stands. Soil temperature is most important in boreal regions (Lippmaa, 1929).

Sunlight may at times be so intense as to cause injury to plants, especially to young seedlings. This injury is generally due to excessive heat or to excessively high transpiration (Shirley, 1936). This type of injury has been studied in coniferous nurseries by Hartley (1918), Hartley, Merrill, and Rhoads (1918), Korstian and Fetherolf (1921), Toumey and Neethling (1924), and Li (1928). Such injuries may also occur in natural reproduction (Baker, 1929). Sun scald of fruit and other hardwood trees has frequently been observed. Sun scald is the result of excessive heating rather than of intense light. The death of trees caused by high air temperature together with poor air drainage occurs occasionally. Much of the so-called winter injury, especially in evergreens, frequently attributed to freezing temperatures, is probably due to excessive desiccation caused by a warm bright day at a time when the soil is frozen rather than to low temperature (Shirley, 1936).

The amount of injury at a given temperature increases with increasing length of exposure and the higher the air temperature the shorter the exposure required to produce death or a given degree of injury (Arthur and Stewart, 1933; Shirley, 1936).

From tests on Norway pine, northern white pine, jack pine, and white spruce 1 to 4 years old to determine killing temperatures Shirley (1936) concluded that: (1) resistance to excessive external heat increased with increasing age and increasing size or mass of plant and tissue; (2) for comparable plants the external killing temperature was higher in air than in water and higher in dry air than in moist air; (3) recovery from excessive heat injury was associated with the capacity to send out shoots from dormant buds on the uninjured stem, white pine and white spruce excelling in this respect, jack pine and Norway pine proving decidedly inferior.

Trees growing in openings, after a partial cutting has been made, are subjected to a much larger amount of effective heat than before the cutting. The increased heat, proportional to the direct sunlight that they receive, has an important bearing on growth. Not only is the temperature of the parts above ground, when subjected to direct light, much higher than when in diffused light but the heat available for

the roots, particularly those in the surface soil, is much higher, owing to absorption of direct sunlight by the surface soil. Li (1926) has shown that the temperature of exposed surface soil in the open at mid-day may be from 20 to 40° F. higher on days with full sunlight than the temperature of exposed surface soil under fully stocked stands of white pine, and even 70° F. higher than the surface soil under litter. The effect of thinning in stimulating reproduction and growth in the openings is due in part to temperature effects, particularly in northern latitudes. In moist cool climates where forest soils become strongly podsolized, exposure of the surface to direct insolation promotes decomposition of raw humus and stimulates nitrification (Hesselman, 1917, 1925).

15. THE LIGHT FACTOR IN SILVICULTURAL PRACTICE

In the practice of silviculture it is desirable to utilize as fully as possible the site factors favorable to increased forest production. Of these the light factor is important not only in connection with the natural regeneration of forests but also in obtaining a maximum production of highest quality timber. Maximum production involves, among other things, the control of stand density so as to make full use of light on the one hand and the control of light intensity on the other to obtain good growth and also to clear stems as a result of the natural pruning of lower branches from the trees in a stand.

The maximum amount of foliage most favorably placed with reference to the light favors volume production, and maximum quality production is obtained when the maximum increment is added to straight, clear, knot-free stems having slight taper (Mundt, 1934). With certain species at intermediate latitudes, assimilation is most efficient at light intensities approximating half sunlight in the middle of the day. This makes it desirable to have the stand composed not only of well-formed, clear-stemmed, full-crowned trees but of not too many per unit of area. Early and frequent thinning is commonly employed in order to control light in the development of more rapidly grown desirable stands (Gehrhart, 1929). Height growth is also stimulated by thinning. The more rapid height growth results in longer internodes of clear stem, in earlier natural pruning of branches and consequently better quality timber. The stand should be thinned to such density that it will receive, at the right time and place, enough light to maintain good growth and to keep it free from the development of undesirable epicormic shoots or undesirable soil conditions.

If a dense undergrowth of shrubs or herbaceous plants comes in under

a stand and chokes out desirable tree reproduction it is evident that full use is not being made of the soil and light. Then it may be desirable to maintain a denser stand. On the other hand, if the soil is bare of undergrowth it indicates severe competition for light and other favorable growth conditions among the trees forming the dominant crown cover.

16. SUMMARY OF RADIANT ENERGY IN RELATION TO FOREST VEGETATION

The effect of radiant energy in relation to forest vegetation may be summarized as follows:

a. Light is necessary for trees and other forest plants to synthesize carbon compounds from carbon dioxide and water; hence there is a minimum light requirement below which trees die, because the energy outgo from respiration is greater than the energy intake through photosynthesis.

b. Although the intensity and quality of light vary widely in one region as compared with another, and at one time as compared with another, the light available in all regions for trees growing in the open is adequate to sustain excellent growth, provided other factors are not deficient.

c. Light is of chief importance in forestry when trees grow in stands because of the shading effect of one plant upon another and the effect of the canopy on intensity and duration of the light which reaches the subordinate vegetation.

d. Under living canopies the intensity of light which reaches the subordinate vegetation varies between wide limits. Even thinned stands hold back a surprisingly high percentage of the full light; beech as much as 80 to 90 percent and fir and pine as much as 60 to 80 percent. Extremely dense unthinned stands may hold back as much as 98 or 99 percent or even more.

e. When the light intensity under canopies is very low and other factors are not more significant, the rate of growth or production of dry matter is almost directly proportional in all species to the intensity; but under higher light intensities some plants increase their rate of growth much more rapidly than others. At the highest intensities a falling off in the growth rate may occur, particularly in the so-called shade plants.

f. The light intensity under forest canopies is seldom so low as to inhibit germination and survival of subordinate vegetation, provided other factors do not become more significant. The intensity, however, determines the rate of carbon assimilation in different species with each

added increment of light, provided other factors affecting photosynthetic activity are favorable.

g. Under natural forest canopies, light intensity at any point fluctuates from moment to moment between wide limits, owing to the multiplicity of openings in the canopy which present a mosaic of light and shade flecks. The total amount of light beneath the canopy probably affects the plants on the forest floor more favorably than the same quantity of light beneath a continuous canopy without openings. It is doubtful, however, whether the fluctuations of light under a forest canopy are sufficiently rapid to cause much increase in rate of photosynthesis above that occurring at the mean light intensity.

h. Because of the effect of radiant energy on the form of forest plants, those growing under canopies are dissimilar in form to those growing in the open. Height growth is retarded by intense radiant energy; hence a progressive reduction in light intensity to the point of a marked reduction in photosynthesis causes a progressive increase in height growth. Trees growing in the shade are usually taller than those of the same age growing in the open, provided other factors affecting growth are not restricted.

i. Although the light under canopies is changed in quality, this change has little effect on photosynthesis in the subordinate vegetation provided the intensity is sufficiently high.

j. Under natural conditions, forest vegetation is exposed to alternating periods of light and darkness, but periods variable in length, depending on latitude and season. The length of daily exposure to light profoundly affects the periods of growth and dormancy and in many plants determines the time of flowering and fruiting.

k. Different species of trees and other forest plants germinate, survive, and grow under varying densities of living canopy. The behavior of each species depends on the amount of incident light at its minimum light requirement and the increase in photosynthesis for each added increment of light. Behavior is also influenced by the extent to which the trees forming the canopy produce changes in the physical factors, such as temperature and soil moisture, that determine the degree to which increased light can be utilized in increased photosynthetic activity. The more important factors other than light which affect carbon synthesis by determining the extent to which an increase in light intensity will bring about an increase in photosynthetic activity are: soil moisture, temperature, CO_2 content of the air, anatomical structure, soil nutrients, atmospheric humidity, and wind movement.

l. Trees forming the canopy not only change the intensity and quality of the light available for photosynthesis in the subordinate vegetation, but they bring about changes in a number of other physical factors upon which photosynthetic activity depends. One or more of these, such as temperature or available soil moisture, may become more significant long before an increase in density of the canopy reduces the light to the point where it becomes more significant.

CHAPTER III

AIR TEMPERATURE

Temperature of the air does not have a striking effect upon the form and structure of trees, nevertheless it is a factor of fundamental importance. The heat requirements of a tree can not be determined by studying its anatomical structure or its form. The action of heat is visible chiefly in its final consequences, that is, in increase, retardation, or complete cessation of physiological processes. We can not directly see whether a tree belongs to the flora of a cold or a warm climate. Plants from hot deserts are often structurally similar and have a strong resemblance in habit to those of cold regions.

Cold causes a tendency in the cone scales of Norway spruce to become broader and shorter (Kjellman, 1885). Warming (1909) states that the leaves of the common juniper in cold climates are appressed; and the senior writer has observed that the leaves of white spruce in Quebec lie more closely against the axis than is characteristic of this species farther south. Other authors contend that the individuals of a species growing in the coldest part of their range are of a deeper color and the foliage is more likely to be tinged with brown. Although there may be some slight correlation between temperature and the structure, form, and color in trees, it is wholly insufficient to give any conception whatever of heat requirements.

Although many physiological researches have been made in recent years to determine the effect of temperature on the vital processes, little information exists regarding species of tropical, polar, and alpine regions. In general it may be said, however, that the resistance offered by different species, varieties, and races to high and low temperature is due chiefly to the inherent peculiarities of the protoplasm and to the admixture of sugar, oils, or resinous bodies with it. In many trees starch changes to fat on the approach of winter and increases the resistance to cold. Fat-storing trees, such as most conifers and birch, are those which grow in the coldest climates (Warming, 1909).

The amount of water present in the tissues of a tree plays a leading part in determining its resistance to low temperature. The resistance is in general inversely proportional to water content. Thus the young succulent shoots of most trees suffer from late frosts; the older lignified shoots do not. Trees and shrubs indigenous to warm regions, when

planted in cold localities, do not receive sufficient heat to harden their tissues; consequently, because of oversucculency, they are killed during the winter. When an unusually hot summer and late autumn bring them sufficient heat to harden their tissues, they withstand low temperature without injury. When tender tissues become frozen, the degree of damage which follows appears to depend somewhat upon the rapidity of thawing. In regions of low temperature many species of woody plants, like birch and willow, develop stems which lie prostrate on the ground and receive a greater amount of heat than they would if erect.

1. SOURCES OF A TREE'S HEAT

The various activities that are continually going on in a living tree involve work. The energy is chiefly supplied from outside sources. Thus a large percentage of the energy from the sun's rays absorbed by a tree is consumed in transpiration, or is returned to the air. Only 1 or 2 percent is consumed in photosynthesis. The mean temperature of trees is approximately the same as that of the surrounding air. Heat is absorbed from the air when a tree is colder and given off to the air when the tree is warmer. The amount of internal heat generated by the life processes is inappreciable. A tree obtains its heat mostly from the sun through the atmosphere. Although the temperature of a tree approaches the temperature of its environment, they are seldom exactly the same, owing to the constant variation in atmospheric temperature and the slow heat conductivity of plant tissues. Thus the deeper tissues of the tree are cooler than the air during the day and warmer at night. Thin, exposed tissues, however, such as leaves and even surface tissues of twigs exposed to the sun, may be warmer than the air during the day and somewhat cooler at night.

2. ABSORPTION OF HEAT BY A TREE

All of the heat available to or in a tree comes directly or indirectly from solar radiation. Even the internal heat generated by the life processes may be traced to this source. When solar radiation falls upon a tree, part of its energy is absorbed and the leaves become warm, often warmer than the surrounding air, in the same way that the surface soil often becomes warmer than the surrounding air. The bole of a tree is probably warmed at its surface by direct radiation more than by conduction from a warmer atmosphere. When the surface is warmed the heat is then conducted to the interior of the stem.

Trees growing in the open begin cambial activity earlier than trees *growing in stands, because the soil under stands is kept cool by the*

forest cover. Trees growing in sand and in other naturally warm soils begin growth earlier in spring than trees growing in cold soils. Cambial activity in a tree growing in a warm soil in the open may begin near the ground before it does in the crown, whereas in a forest it usually begins in the crown. This difference is probably due to differences in soil temperature. As a rule, shallow-rooted trees begin their spring growth earlier than deep-rooted ones, owing to differences in temperature in different layers of the soil. Warm spring rains stimulate trees to rapid growth. A mulch prevents rapid warming of the soil in spring and retards the starting of growth in vegetation.

3. INJURIOUS EFFECTS OF HEAT

It is seldom that a tree beyond the seedling stage is quickly killed or even seriously injured by high air temperature. However, the resistance of plant tissues to high temperatures is quite probably affected by high osmotic concentration of the sap and low water content.

An unfavorable temperature is manifested in an unhealthy development and predisposition to death through disease. The sudden exposure of the boles of forest trees having thin bark often results in death of the cambium on the exposed side. This is called sun scald.

4. INJURIOUS EFFECTS OF COLD

Trees suffer direct damage from frost. Ordinarily, native trees are not killed outright by cold winters, but frequently suffer damage from frosts occurring late in the spring after vegetative activity has begun. Damage by late spring frosts is most common in young seedlings, particularly when grown in the open. In some areas the injury to seedlings is so great that it is very difficult to establish a stand without sheltering trees to check rapid radiation and prevent sudden thawing. Injury by late frosts is due to the direct action of the cold on the delicate tissues of newly developed leaves and twigs. It may to some extent be due to the sudden thawing of frozen tissues. Trees in the shade are not injured by late spring frosts as badly as those exposed to direct sunlight. Trees introduced into a region from a warmer climate not only are damaged by spring frosts but they suffer from early autumn frosts and are often winter killed. The ends of the branches may be killed in the autumn because frosts come before growth is completed and the tissues hardened.

The frost-resisting power of the various indigenous species has not been adequately studied, chiefly because reproduction is for the most part in relatively small openings in forests where there is natural pro-

tection, and seedlings have not been tested on extensive clearings. It will doubtless be found that the loss of reproduction from frost is far greater than is generally believed.

5. EFFECT OF TEMPERATURE ON DIFFERENT PLANT FUNCTIONS

The life of a tree is made up of many interrelated activities, each of which is performed within its own range of temperature. A tree succeeds best when all its functions are in a state of equilibrium that corresponds to the external conditions.

A knowledge of the extreme temperatures at which a given organ will function is of far more importance in forest distribution than a knowledge of the temperature at which it functions best. The ecological optimum is not the same during the entire growing season. Thus the temperature which is most favorable for germination and the swelling of buds is not the optimum for succeeding functions. The optimum for flowering is much lower than for fruit ripening. Few studies have been made to fix optima of the different functions.

It is chiefly low temperature during the hottest 4 months of the year that causes the limitation of forests at northern and southern latitudes and at high altitudes. In some places timberline is caused by absence of moisture, by poor soil conditions, or by exposure to storms, but as a rule it is determined directly or indirectly by air temperature. It is not, however, a question of low winter temperature, but of low summer temperature.

Were species not restricted in their distribution by heat requirements, there would be a very general distribution of each species over the entire country. Species now in the tropics would migrate into temperate and arctic regions were they not prevented by cold. Cold-region species would spread throughout the warmer regions were it not for the fact that they are adapted to a long winter and a short summer, and do not survive when transplanted to localities having different temperature conditions. The northern limit of a species is in part an isotherm beyond which it can not exist because of winter killing and frequent injury from early and late frosts. Most frequently it is the limit of reproduction. That is, temperature conditions are so unfavorable that natural reproduction is wanting or so scanty it can not compete with the reproduction of other species for which the temperature is more favorable. In the same way the southern limit of a species is in part an isotherm beyond which it can not survive.

Although all species of trees and all plant communities appear to

have rather well-defined critical temperatures, beyond which they do not extend, there are great differences in species and in communities in the climatic distributional space of each. Some species and some communities are confined within rather narrow temperature limits; others are far less exacting and as a consequence extend over a wider range of latitude and altitude.

Individuals of all species which occur on the outskirts of their range occur singly or in isolated groups where local temperature conditions are suitable. The extension of a tree species into a colder latitude or to a higher elevation occurs only in warm local situations as expressed in southern aspects. Its extension into a warmer latitude or to lower elevations occurs only in cold local situations. When seeding or planting is done at the northern geographical range of a species, or farther north, or when an exotic species is introduced from a warmer region, warm local situations should be selected as expressed in southern and western aspects. At the southern geographical range, or when an exotic species is introduced from a colder region, cold local situations should be selected, as expressed in northern and eastern aspects where the air and soil are cooler.

6. CRITICAL TEMPERATURES FOR FOREST VEGETATION

Although the reason is not known and no adequate structural differences are correlated with heat requirements, observations indicate that the various tree species can live only at temperatures between two extremes. These extremes are at variable distances apart for each species. The temperature extremes at which a species persists may be termed its critical temperatures. So also the extremes at which a certain type of vegetation exists may be termed the critical temperatures for the particular type.

Within a certain range, metabolic processes are more active at higher than at lower temperatures. Assimilation, within certain limits, increases with temperature according to the van't Hoff law. As the temperature rises above a variable point, it appears to have a progressively deleterious effect on protoplasm; raised still higher, it produces death almost instantly (Skeene, 1924).

7. Lower Critical Temperatures

Species, varieties, and races exhibit great variation in their ability to withstand low temperatures. Thus many tropical plants are killed if the temperature falls as low as 41° F., but many arctic species will withstand a temperature as low as —76° F. for a part of the year

(Schimper, 1903). This is true of certain poplars, willows, spruces, and firs. Plants of arctic regions, however, are nearly as sensitive to cold during their growing season as are plants of warm regions. In warm regions the freezing of a plant at any season of the year usually results in death. Microscopical examination shows that the intercellular spaces normally filled with air contain ice crystals which were formed at the time of the freezing of the plant tissues and at the expense of the sap of the surrounding cells. This loss of water from the cells, together with the upset of the colloidal system, may be regarded as the cause of death, although cold in itself may exert a directly injurious influence on the protoplasm. Seeds are usually low in water content. It has been found by experiment that certain dry seeds like those of pine and spruce can safely withstand the temperature of liquid air. Death from cold may result when low temperature prevents a tree from absorbing adequate moisture to sustain the transpiration current, especially if the soil is frozen around the tree roots. So far as known there is no place on earth where the temperature falls so low that trees can not exist. The complete absence of tree growth where temperature is the most significant factor is due to continued cold, not to the minimum temperature at a particular time.

The point at which low temperatures become critical varies widely, depending on the condition of vegetation. Plants, the tissues of which are properly hardened and prepared for subzero temperatures, are resistant to injury by freezing. Many conifers thus conditioned for low temperatures may withstand —40 to —50° F. in the winter. On the other hand, the same trees caught by a sudden freeze in the late spring, when the tissues are succulent because of rapid new growth, the presence of a large amount of free water, and dilute cell sap, may be severely injured at temperatures only a few degrees below freezing.

A striking example of severe injury to forest vegetation under such conditions occurred in the Wasatch Mountains of Utah in May, 1919 (Korstian, 1921). Following the warmest May weather in 18 years a sudden cold wave caused the temperature to drop from a maximum of 78° F. to 15° F. within a relatively few hours. The season being from 2 to 3 weeks earlier than normal, all growth was far advanced. Wholesale injury to the tender, succulent tissues and even to older growth on shrubs and hardwood trees resulted. Of the native conifers, firs — Douglas fir, alpine fir, and white fir — were injured to a greater extent than spruces. Occasional alpine firs as large as 18 inches in diameter and 65 feet tall were completely killed, even though during the preced-

ing winter they had successfully withstood many days of subzero weather. Pines were either uninjured or only slightly injured.

8. Upper Critical Temperatures

The power that various trees have for resisting heat also varies with the species and, to some extent, with varieties and races within the species. The variation in trees in their capacity to endure an excess of heat above the optimum for the species is not nearly so great as the variation in their power to resist cold. Seeds, when thoroughly dried, often safely resist a temperature of 158° F. without having their viability impaired, and for a short time a temperature as high as 212° F. Succulent plants, or plant tissues and plants in active growth, are very sensitive to a rise of but a few degrees above their optimum. Thus a number of garden plants were uninjured when exposed for a long time to a temperature of 95° F., but a rise to 104° F. for a few days or to 113° F. for a few hours was fatal. On the other hand, the flora of hot springs thrives at a temperature of 140° F. and in some instances at even higher temperatures. In parts of India the air temperature sometimes rises to 122° F. and parts of plants exposed to the sun's rays often are heated to from 140° F. to 158° F. However, the actual killing temperature, or thermal death point, for leaves of many plants occurs at or near 122° F. Leaf temperatures may be several degrees in excess of that of the surrounding air without being lethal. Comprehensive studies on the temperature of leaves under varying atmospheric temperature, humidity, and light indicate that, contrary to common belief, transpiration has only a minor effect in reducing leaf temperature (Clum, 1926).

For any given light intensity a critical temperature probably exists which for a given species should be possible of prediction. The same type of relationship between total amount of energy absorbed and that released through oxidation is shown by a steady increase in top-root ratio with increasing temperature (Davis and Hoagland, 1928). Apparently there is less excess carbohydrate material at the higher temperatures, and the roots, owing to their location, are the first to be restricted in the use of the excess for tissue formation.

9. Species in Relation to Critical Temperatures

Wherever the mean air temperature during the 4 hottest months of the growing season falls as low as 50° F. forests become scrubby in character, no matter whether the temperature results from latitudinal

or altitudinal position. A prolonged low temperature during the growing season is not equivalent to a higher temperature of shorter duration. Thus the total amount of heat during the growing season is not a safe guide to the silvicultural heat requirements of a species.

Mayr (1925) states that throughout the northern hemisphere the arborescent genera are generally the same wherever the length and temperature of the growing season are similar. He concludes that if the temperature of any locality for the 4 hottest months of the year is known, it is possible to determine what species from other regions, where the temperature is also known, can be introduced in forestry practice, provided moisture conditions are suitable.

10. Individuals in Relation to Critical Temperatures

Although species have well-recognized critical temperatures, these temperatures do not appear to be uniform in the individuals which comprise a species. With species of wide distribution it is not sufficient to know simply the general temperature requirements of species. Thus stock grown from hickory and walnut seed collected in southern Missouri or farther south will not survive the climate of Minnesota and New York, whereas stock grown from seed collected farther north is perfectly hardy. Stock grown from seed of Douglas fir collected in California is not hardy in New England; stock of the same species from Colorado is much hardier. The indigenous black oak is hardy in Connecticut. Seeds of this species collected in Oklahoma, when planted at New Haven, produce plants which do not survive the first winter. This is of more than passing importance to foresters because success in seeding and planting, even when the best species are used, often depends upon the source from which seed is obtained.

As a rule, forest trees should not be seeded or planted in a region much colder than the area where the seed is collected, even if the limit of distribution of the species is much farther north. Experience has demonstrated that transplantation from a warmer to a colder site is almost always unfavorable. On the other hand, present evidence indicates that most trees remain healthy when transplanted to a site somewhat warmer than their native home. Seed used in silvicultural practice should come from slightly colder rather than from warmer regions as compared with those where the seeding or planting is done. Seeds coming from a warmer region usually produce trees which are severely injured or killed by frost, because the young tissues seldom mature by the end of the growing season. Trees moved from a colder to a warmer site often start a second growth in the autumn which

destroys the buds, particularly the flower buds. Such trees are usually precarious seed bearers.

Trees in the juvenile stage are much more subject to injury from cold than older trees. Serious injury is often prevented by starting a young forest under an old stand. The effect of the overstory is to render temperature conditions under it more uniform and thus less harmful to young trees.

11. EXTENSION OF A TREE'S RANGE

The limits of the natural range of a species are largely a matter of its capacity to reproduce. The range of a species can usually be extended by planting but, when so extended, it does not reproduce and, in time, the natural range is reestablished although the trees may live and grow to fair size.

When trees are planted in localities where the climate is warmer than in their natural home, growth is at first stimulated, the wood is usually inferior, the bole-form is poor, and usually there is exhaustion and death. Thus when Norway spruce is brought from northern Europe to the lowlands of Belgium and northern France, its growth is very rapid at first but falls off early. It bears many barren cones, is usually attacked by disease or insects, and dies before it reaches merchantable size. Present indications are that it will have much the same life history when planted in southern New England.

12. AIR TEMPERATURE AND FOREST VEGETATION

Air temperatures directly affect growth. This is not always apparent when only periodic and mean temperatures are considered. Maximum temperatures in particular appear to be most important in fixing the temperature requirements of species and plant communities. Maxima that can be tolerated without destructive reactions in a tree have been inadequately investigated. The air temperature requirement of a given species is greatly modified by solar radiation. Thus a tree growing in the open requires a lower air temperature than the same species growing under shade. In the former case the tree is heated not only by air temperature, but also by the heat of solar radiation.

Merriam (1898), in his comprehensive study of air temperature zones as affecting forest distribution and growth forms, concludes that air temperature is the most important single factor in fixing the limits beyond which particular species and particular communities can not extend. His studies suggest that the northern distribution of terrestrial plants and animals in the northern hemisphere is governed by the sum

of positive air temperatures for the entire season of growth and reproduction, and that the southern distribution is governed by the mean temperature of a brief period during the hottest part of the year. Bates (1924), Pearson (1920, 1931), and Shreve (1915), who have studied the altitudinal distribution of species in certain mountain ranges in the western United States, conclude that temperature controls the upper limit of distribution. The local occurrence of species within certain altitudinal belts may be determined more by other factors than by temperature (Baker and Korstian, 1931).

Owing to the temperature at the surface of soil exposed to direct solar radiation being much higher than the temperature at various heights above the surface, the effect of insolation on the survival of seedlings that germinate in the open is often very marked (Hartley, 1918; Korstian and Fetherolf, 1921; Toumey and Neethling, 1923; Bates and Roeser, 1924). Various species of spruce and fir, and to lesser extent other conifers, are often killed by excessive heat at the soil surface shortly after germination takes place and before the stem has thickened and become woody. Lesions are formed on the tender stems at the surface of the soil, the transpiration current is cut off, and the plants bend over and soon wither and die. This manner of injury from heat is not confined to seedlings in their earlier stages of growth. It may continue, but with less severity, until the plants are two or more years old. It is often a conspicuous cause of injury to young advance growth after clear-cutting.

13. ACCLIMATIZATION

Although the extremes of temperature are reasonably constant for individual species, the cardinal points for separate functions vary with climatic conditions, that is, the extremes for the separate functions are capable of displacement either upward or downward, so that when a species is transferred from one area to another with a different temperature, if the climatic change is not too great, it may adjust itself to a new environment and become acclimated. This possibility varies with different species. The extent to which this is possible with some species appears almost unlimited; with others, and especially trees, if it takes place at all it is only between very narrow limits. A species may grow in a region outside the area of its natural distribution and still not be acclimated. Complete acclimatization is possible only when the cardinal points of all functions change in harmony with the new temperatures. Thus many plants from cold regions exhibit rapid and vigorous vegetative growth in the tropics, but reproduction is usually entirely

wanting. The species has been able to change the cardinal points for vegetative growth, but not for blossoming and fruiting. On the other hand, many trees of warm regions grow in cooler regions but do not produce flowers and fruit. Light, as well as temperature effects, however, enter into this reaction.

A question of practical importance to foresters in the study of the relation of trees to heat is the introduction of exotic species. One often hears the question of acclimatization of exotics discussed. Thus a European tree is planted in this country and if it grows well it is said to be acclimated. If it does not grow, the layman has an idea that through selection hardy varieties may be developed. It is hardly proper to say that a tree becomes acclimated when the conditions in which it finds itself in its new home are similar to those in the place from which it came. It would be unnatural if it did not grow. *The term acclimatization refers to the acquisition of new inherent qualities or tendencies through the influence of a different environment.*

Sometimes a tree suffers from cold when young and later in life appears to be perfectly hardy. This is because in youth the roots and crown are near the surface, where the extremes in temperature are greatest. Later in life the crown is farther above the ground, the roots are deeper in the soil, and the tree is firmly established. In this case it is not a question of adaptation to climate, but rather development in the individual. Frost resistance is developed through natural selection. This is proved by the fact that there are hardy races as well as sensitive races of the same species. Seed from trees growing in localities with a naturally severe climate produce trees more frost-hardy than seed of the same species from the warmer portions of their range.

A forester should take advantage of hardy races when he is planting in a region where there is danger from frost, and should use seed from that portion of the tree's range having a rugged climate.

CHAPTER IV

ATMOSPHERIC MOISTURE

The amount of moisture in the air is one of the chief factors influencing forests. Atmospheric moisture is the immediate source of supply for precipitation which may occur in the form of rain, snow, sleet, hail, or dew. Therefore, precipitation along with atmospheric humidity and evaporation are important factors in influencing the distribution, occurrence, growth, and development of forests. They are also important in determining the ecological significance of water in the life of forest trees.

1. WATER AND VITAL PROCESSES IN TREES

Water is fundamental to the vital processes of trees. Its significance to trees is as follows:

1. Water is present in all protoplasm and in all cell walls.
2. Water, as cell sap, occurs in cell vacuoles where it plays an important rôle in turgidity and growth.
3. Water is directly assimilated.
4. Water induces absorption, osmosis, and the transfer of materials.
5. Water is essential to the assimilation of carbon which is retarded in non-turgid plants and ceases in wilted plants.
6. Water is necessary for respiration, which ceases when reduced below a certain minimum.
7. Water is necessary for transpiration.
8. Water is necessary for all movements due to swelling and irritability.

The amount of available water present determines the possibility of a tree's remaining alive. Although death ensues from lack of water, there is great variation in trees and their parts in the degree of desiccation that they can withstand and still remain alive. The water in the atmosphere and soil is of the greatest influence in shaping the external and internal structure of trees. There is no other influence which causes such profound differences in forest vegetation as do differences in the supply of available water. Water comes in contact with a tree in two ways, namely, through the air and through the soil. Humidity mainly controls water loss from plants. Water content of the soil chiefly determines water intake. Humidity as a stimulus chiefly affects the parts of a tree above ground and exposed to the air. The leaf, which is the assimilating organ, is the most sensitive part of the shoot. Indirectly, humidity affects the parts below ground through its influence

upon the soil, more particularly upon its water content. Soil moisture as a stimulus affects the parts of a tree in the soil. The younger roots and, where present, the root hairs near the ends of the root ramifications are the absorbing organs and the most sensitive parts of the root.

2. PRECIPITATION

The water requirements of trees are chiefly met by the precipitation of the water vapor of the air in liquid form as rain and dew, although snow in some regions may contribute considerable water during the spring. Whenever the air is cooled to the dew-point, or to the point of saturation, so that it can not hold all the water in it in a vaporous state, the water is deposited in one of the three forms of atmospheric precipitation, namely, mist (clouds), rain (including the frozen forms known as hail and sleet), or dew (including hoarfrost). Atmospheric precipitation is of particular importance in its effect on vegetation, owing to its relation to atmospheric humidity and water content of the soil.

In particular, fluctuations in water content of the soil are directly traceable to variations in precipitation. Aside, however, from the basic beneficial influences of precipitation in adding to the supply of water available for absorption by forest vegetation and through its effect on humidity in checking the loss through transpiration, precipitation directly influences forest growth through its mechanical action on the trees themselves and on the soil. This influence of precipitation is modified by the rapidity of descent and the amount falling during single storms.

In order for precipitation to be absorbed by the parts of plants above ground the surface cell walls must be permeable and the epidermal cells must contain osmotically active substances; furthermore, the water must not flow off their surface too rapidly. Many of the simpler or more primitive plants, as lichens and most mosses, obtain most of their water in this way. Among the higher plants some species have special structures for absorbing water from atmospheric precipitation. Some of these structures are: aerial roots with special absorbing tissue and epidermal hairs capable of taking up water (Warming, 1909). In general, however, the parts of woody plants above ground seldom absorb water from atmospheric precipitation. Absorption by the roots is the normal necessity of all trees. Most plants are adjusted to a definite average amount of precipitation, which in general varies with the species. Many trees in extremely wet regions appear to have structures for the removal of rain. Some species have their foliage covered with a wax or bloom which makes them unwettable.

Mist (clouds) absorbs light and retards heating of the soil. Against

this there is no protection. Barren lands and poorly developed vegetation in cold coast regions are often directly due to the presence of almost continuous mists. Aridity shortens the vegetative period and hastens blooming and the maturing of seed. It often causes a marked resting period irrespective of temperature conditions. Many trees and other plants protect themselves against a regularly occurring drought in the growing season by shedding their leaves and putting forth new leaves with the renewal of precipitation. This is true of certain trees in southern Arizona and is the chief cause of the deciduous character of certain trees in India.

Variations in the geographical distribution of precipitation influence markedly the distribution of forests. With the same amount of annual precipitation the character of a forest depends upon whether the rainfall is in the growing season or in the cold season; whether it is evenly distributed or confined to a few months of the year. In fact the distribution of precipitation throughout the year, especially where rainfall is not heavy, may determine whether a forest is present or a type of vegetation needing less water. Precipitation occurring during the winter is less effective than summer rainfall, although some precipitation in the winter is desirable. Baker and Korstian (1931), in a study of rainfall in the 11 far western states, observed great variation in annual precipitation in these states, ranging from 15.5 inches in Montana, where the heaviest rainfall occurs in the summer, to 45.5 inches in California, where the summers are dry. They suggest that differences in forest growth may be caused rather by the seasonal distribution of precipitation throughout the year than by total rainfall.

Although an average of 15 inches of precipitation per year is sufficient to support a forest of ponderosa pine in Montana, a mean annual rainfall of 20 inches or more may be necessary for the same species in New Mexico, owing to the higher temperatures, lower atmospheric humidity, and particularly the higher vapor pressure deficit. Other similar examples could be cited.

The precipitation from the moisture-laden westerly winds that blow over the Pacific Ocean accounts for the more luxuriant forests on the Pacific slope of the Cascade and Sierra Nevada Mountains than on the interior or eastern slope. In the great semi-arid interior region forests are confined to the mountains and higher plateaus where snow and rain occur, in any abundance, generally above the height of the Cascade and Sierra ranges.

The extensive forests of the eastern United States are capable of existing in spite of the generally unfavorable and at times excessively

desiccating conditions of the Great Plains (Zon, 1913). During the summer when the eastern forests are most in need of water and when a prevailing westerly wind would be most harmful, southerly winds, largely replacing the drying westerlies, bring in moisture from the Gulf of Mexico and the south Atlantic Ocean. These southerly winds, unobstructed by high mountain ranges, spread widely over the eastern half of the continent, with the result that precipitation there is somewhat heavier during the summer than in the winter. Even when no precipitation occurs these winds are more humid and retard evaporation and transpiration more than the dry westerly winds.

On the Laramie Plains in Wyoming and in similar situations in the West, the chief obstacle to forest growth is the absence of a protective snow blanket in winter. As a result, the high, desiccating winds, which thoroughly dry out the surface soil, and the intense cold kill young trees outright or severely injure them.

In northern regions all species survive the winter in much better condition when the ground is covered by snow than when unprotected. In general, the amount of snowfall and the length of time that it covers the soil during the period of winter dormancy profoundly affect forest vegetation. The snow cover has a far-reaching effect on the supply of soil moisture. When a thick blanket of snow falls with the approach of winter, it prevents the soil from freezing and as the snow melts next to the soil surface, water seeps into the soil. Thus the soil is kept loose and friable, and roots continue to grow and absorb moisture as needed to replenish that lost through winter transpiration.

Precipitation, which is the chief determinant of soil moisture, has frequently been found to have a positive correlation with tree growth. The most rapid height growth of western larch seedlings in northern Idaho occurs during the moister and warmer seasons (Brewster, 1918). Height growth of ponderosa pine in the Southwest has been found to be correlated closely with April and May rainfall (Pearson, 1918). The same relationships were found to obtain for ponderosa pine and Douglas fir in central Idaho (Korstian, 1921). Douglas (1928), as a result of intensive studies on dry-climate conifers, found that the annual fluctuations in diameter growth are correlated with rainfall variations. Coile (1936) found that the total precipitation during January to May, inclusive, February to April, inclusive, and April to June, inclusive, gave the highest positive correlation with the annual diameter growth of loblolly pine in southwestern Louisiana, of slash pine and longleaf pine in the Coastal Plain of Georgia, and of shortleaf pine in northern Arkansas, respectively.

Abnormally low precipitation, especially during the growing season, may cause deficiencies in soil moisture so serious as to result in the death of trees in natural stands and plantations (Hursh and Haasis, 1931; Shirley, 1934). Exceptionally severe droughts may even destroy entire stands.

Winter killing is often due to the ground's freezing solid, thus making water intake by the roots impossible at times when warm, dry winter winds cause loss of water from the parts of the plants above ground. It is notable that regions having a cold winter climate but without a protective blanket of snow are naturally without forest vegetation. A snow blanket not only affects soil moisture and freezing of the soil, but it also protects tree reproduction and lesser vegetation from adverse winter conditions. Alternate freezing and thawing, which is characteristic of soil in winter, unprotected by a snow blanket, causes heaving of young plants and, as a consequence, death or severe injury (Haasis, 1923).

Although snow in winter is generally of great benefit to forest vegetation, under particular conditions it may be destructive to reproduction and young growth. When it forms drifts, which become compact and icy, it is slow in melting in the spring and the young trees and other vegetation are likely to be smothered. Young trees may also be killed by so-called snow-smothering fungi working under the snow (Korstian, 1923).

3. Resistance Offered by Trees to Mechanical Injury from Precipitation

Variation in the resistance of various species to injury from precipitation is in some localities sufficiently pronounced to warrant the selection of species in seeding and planting with this point in view. Furthermore, the mechanical action of precipitation upon the soil is often so important that it determines the silvicultural method to be followed in the management of a forest. Violent and prolonged downpours of rain, although directly harmful to the foliage of species having large, thin leaves, are chiefly injurious because of their mechanical action on the soil. They result in eroding and washing away the litter and humus and exposing the mineral soil on unprotected slopes. Seedlings and seed beds are injured and young plants washed out.

Regions of scanty rainfall usually suffer most from the mechanical action of rain, both on vegetation and soil, because a large part of the annual precipitation occurs during a few storms of large and rapid downpour. In most parts of the eastern United States rainfall is fairly

evenly distributed over the year, and violent storms are the exception rather than the rule. In parts of the West, however, the opposite is the rule and special attention must be given to overcoming the harmful effects. So far as the direct harmful effect upon a stand itself is concerned, this can be counteracted by selecting species having small, thick leaves better adapted to resisting injury from the mechanical action of rain. In these regions, too great emphasis can not be placed upon the necessity of maintaining forest growth upon all soils subject to excessive erosion when unprotected. Forest growth checks the velocity with which rain strikes the soil and extends the period of time before which it reaches the ground. The wealth of lesser vegetation on the forest floor and the layer of litter, moss, and humus hinder the speedy runoff of water and consequently lessen erosion. In general, forest growth should be removed gradually from steep hillsides and young growth started some years before all the old timber is taken away. When forests are started by seeding or planting on bare slopes and on other sites subject to excessive erosion, special means must be devised to keep the soil in place and prevent damage by the washing out of seeds and young plants. When it is necessary to make seed beds on sloping ground, they should be small and made level by terracing. When seeding is done on unprotected slopes, the seeds should be sown along contour lines, never in lines running up and down the slope. When planting is done in furrows, the furrows should follow contour lines. Erosion can be checked by a series of parallel ditches or terraces which follow contour lines and are more or less broken to prevent water from flowing in them. These should be from 6 to 18 inches deep, and at intervals of from 15 to 40 feet. They not only serve to check the flow of water but are of great additional use in dry regions because they retain the surface flow and permit it to sink into the soil gradually.

4. Mechanical Action of Snow on Forest Growth

In most mountain regions the mechanical effect of snow upon a tree itself is far greater than that of rain. The effect upon the soil, however, is much less and strikingly different in that snow serves an important function as a soil cover, thus protecting the young growth from adverse climatic conditions and the soil from excessive freezing and drying by cold winter winds (Jaenicke and Foerster, 1915). Both single trees and stands exhibit wide variation in the degree of resistance which they offer to the mechanical action of snow. The degree of injury depends upon the species, age of trees, and density of the canopy. In many regions this injury may be so serious as to make it necessary to give it

careful consideration in the selection of species for artificial regeneration and in deciding upon the silvicultural system to practice in the management of the crop.

Avalanches, particularly ground and top avalanches, are very destructive to forests in high mountains. The ground avalanche forms when the snow field on a steep slope breaks loose from the snow mantle above and slowly moves over the slope to lower levels. The top avalanche differs from the ground avalanche in that the snow field slips or slides over a crust of older snow.

Snowbreak is caused when the weight of snow exceeds the resistance offered by a tree. Stems and branches are so badly bent that they do not later regain their normal position. Conifers offer a much larger surface for the accumulation of snow and are more subject to injury from this cause than deciduous species, although the latter are by no means entirely exempt. Pure forests and those of even age are much less resistant to this manner of injury, consequently most natural forests exhibit less injury than stands established by seeding and planting. The more irregular and varying the level of the canopy, the less the amount of snow held back and consequently the less the damage.

5. Mechanical Action of Sleet and Glaze on Forest Growth

Sleet or glaze, although occurring at infrequent and irregular intervals, often exerts a greater mechanical action on forest vegetation than snow, although the manner of injury is the same. This injury is most prevalent on north and east slopes in mountainous regions. The degree of injury depends very largely upon the species of trees; consequently in regions where sleet storms are of common occurrence, species subject to excessive injury from this cause should not be selected in artificial regeneration. Species with slender boles, large crowns, numerous and brittle branches, and abundant winter foliage are most subject to injury. Boxelder, gray birch, silver maple, and chestnut are particularly subject to this manner of injury in New England. Elm, hackberry, hemlock, and hickory are very resistant.

The coating of ice which forms when cold rain comes in contact with surface soil, trees, and other objects, the temperature of which is at or below the freezing point, is known as glaze. Such glaze storms may do great damage to trees. A heavy load of ice coating trees causes large numbers of them to overturn or to break off, especially when a strong wind accompanies a glaze storm or follows it before the ice has melted. Pine stands on the Piedmont Plateau should not be thinned too heavily on account of glaze storms that occur occasionally in this region. When

grown in dense stands pines are tall and slender and will be bent over or snapped off under the weight of a covering of ice on the foliage and branches. If openings in the crown canopy are not made too large, there is a tendency for the trees to support each other, thus holding the loss from ice damage to a minimum (Korstian and Maughan, 1935).

Glaze or ice storms are unfortunately not infrequent in the southern Appalachian Mountains. Although the same species that are susceptible to damage by sleet and snow are also generally subject to ice damage, Rhoades and Ashe (1918) report that apparently no one species withstands the shock of the ice load better than any other in severe ice storms in the southern Appalachians. They also show that breakage by ice is a predisposing cause of diseased timber. Later observations by Abell (1934) indicate that white pine and hemlock appear to be highly resistant to glaze-storm damage. Scarlet oak is a frequent victim, many red maples are severely injured, and black locust suffers heavily; white and black oaks are intermediate in resistance.

6. ATMOSPHERIC HUMIDITY

Atmospheric moisture which is in the form of water vapor is commonly known as atmospheric humidity. When considered in connection with certain other environmental factors, it affords a reasonably close indication of evaporation and consequently the rate of transpirational water loss; the drier the air the greater the water loss. Within certain limits all environmental conditions which reduce atmospheric humidity, such as high air temperature, high winds, and intense solar radiation, increase transpiration. Atmospheric humidity is commonly expressed as *relative humidity, which is the percentage of saturation of the air.* It largely governs the absorbing or evaporating capacity of the air. A roughly inverse relation exists between relative humidity and evaporation and transpiration, that is, as relative humidity increases transpiration decreases. Where a more direct relationship is desired the *saturation deficit* is sometimes used. Saturation deficit is the amount of water required at any time to saturate the atmosphere completely and cause condensation. In short, *it is the difference between relative humidity and saturation expressed as a percentage,* that is, air having a relative humidity of 60 percent would have a saturation deficit of 40 percent. Of still greater ecological significance is the *vapor pressure deficit* expressed in inches or millimeters of mercury. *It is the difference between the highest possible vapor pressure and the actual vapor pressure.* It gives a direct indication of the atmospheric humidity conditions as influenced by temperature. Re-

cently Livingston and Shreve (1921), Bolas (1926), Braun-Blanquet (1932), and Anderson (1936) have stressed the importance of the vapor pressure deficit as a good measure of atmospheric moisture conditions, because it may vary greatly with changes in temperature even where relative humidity or the saturation deficit remains constant or varies

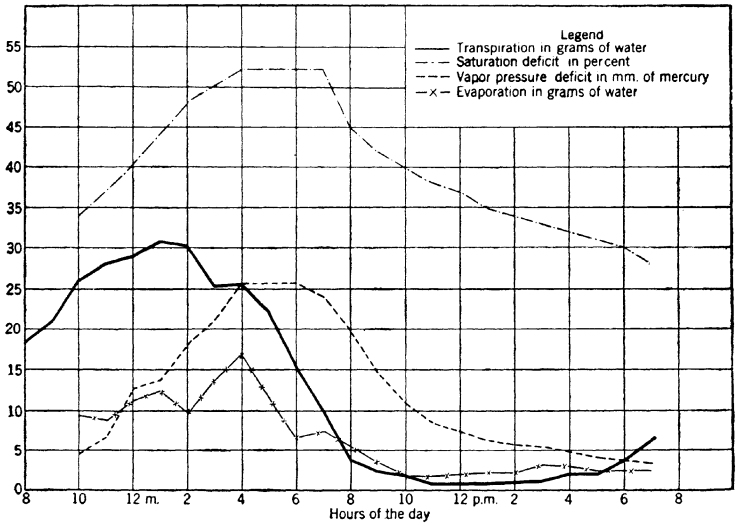


FIG. 5.—Diurnal variation in transpiration of 8-year-old white pine in relation to evaporation and to the saturation deficit and the vapor pressure deficit of the air. (*Adapted from Dole, 1924.*)

but little. Also, owing to its increase with temperature, it gives an indication of the evaporation rate (Fig. 5). The effect of wind on evaporation is also demonstrated through its influence on the steepness of the diffusion vapor pressure gradient. After superimposing isoclimatic lines of vapor pressure deficits over a vegetation map of the United States as modified from Shantz and Zon (1924), Huffaker (1942) also concludes that vapor pressure deficit is a more critical ecological factor than relative humidity. He found a superior correlation of the vapor pressure deficit curves over the relative humidity curves with the boundaries of vegetation types.

No other factor is so thoroughly clear in its influence upon tree life as water. The progress of water can be followed, step by step, from its entrance through roots to its exit through shoots. Although the stimulating effect of atmospheric humidity is chiefly confined to shoots and

that of soil moisture to roots, they both work together in determining vegetation, and in reality they are two phases of the same stimulus (Clements, 1905). The various form and structure modifications due to the degree of absorption cannot be directly referred either to moisture of the air or to soil moisture, but to the two together. Thus a dry atmosphere and a relatively abundant absorption may cause the same modifications as a moist atmosphere and a relatively small absorption. The rate of growth is not correlative with the rate of transpiration.

Woody species thrive on the western slopes of the coast mountains of southern California where subject to frequent fogs and a relatively humid atmosphere. Farther inland a similar vegetation is possible only when a much larger amount of water is available for absorption because of the less humid atmosphere and correspondingly higher evaporation rate. The amount of water required for absorption by a given species depends largely upon the amount emitted to the air through transpiration. The greater the humidity the less the required absorption.

Xerophytes have been defined on the basis of site and on the basis of anatomical and physiological characteristics. Kamerling (1914) attempted to establish a purely physiological criterion for xerophily. As it involves the reaction of a plant to its environmental complex it can not be adequately defined in terms of habitat, of anatomy, or of physiology alone. It has been defined for the most part on inferences derived from anatomy.

The influence of water is so great that ecologists designate a vegetation which corresponds with physiological wetness as *hygrophilous* and one which corresponds with physiological dryness as *xerophilous;* these two forms are connected by all gradations (Schimper, 1903).

Physiological dryness and wetness do not correspond with physical dryness and wetness. They are not the result of the relative amount of moisture in an environment but of a combination of all factors which reduce absorption and increase transpiration on the one hand and which increase absorption and decrease transpiration on the other.

7. Effect of Variations in Atmospheric Humidity on Forest Vegetation

There is always some moisture in an invisible gaseous state present in the atmosphere. All sites, however, vary greatly at different times in the amount present, measured in percentage of saturation. When the air becomes completely saturated, part is eliminated through precipitation. How much water the air will hold before complete

saturation and consequent condensation depends on the temperature. Cold air will not take up so much water in its invisible gaseous form as hot air; consequently, great fluctuations occur at different times during the day and at different seasons of the year.

It is not the actual amount of invisible moisture in the air which affects tree life but the amount required for the air to become saturated. The amount of water in the atmosphere determines its absolute humidity. The latter is the actual amount of water by weight present in a given volume of air. A decrease in temperature increases relative humidity without increasing absolute humidity. An increase in temperature decreases relative humidity. The vapor pressure deficit determines how rapidly water is taken up by the air from the moisture present in the surface soil and on vegetation and on water surfaces. It determines what is commonly called dryness of the air; consequently, it is one of the indices, and usually the most important one, of the evaporating energy of climate. As transpiration depends largely upon relative humidity of the air, it is much greater during the day than at night, owing to the higher temperature and consequent lower relative humidity. It is also greatly influenced by solar radiation. In regions where atmospheric humidity is high and fogs are frequent, there is much condensation on the foliage. This may drip to the ground and add to the water supply of the soil.

Where soil moisture conditions are suitable, there is no known region where the air is too dry to sustain forest growth. Thus in the most arid regions, forest trees of one species or another thrive when the soil is supplied with water through irrigation. All species, however, have not the same power for resisting a dry air even when the soil is adequately supplied with moisture. Thus most species with large transpiration surfaces, thin cuticle and other hygrophilous structures, fail when planted in desert regions under irrigation. Roots are unable to supply a translocation current of sufficient volume to overcome the loss through transpiration.

There is a wide range in the variations in humidity under which different species of trees will thrive. Thus species like Douglas fir, red cedar, and cottonwood appear to thrive in regions having a wide range in relative humidity. On the other hand, redwood appears to be limited in its distribution to the coast region in Oregon and California, characterized by frequent fogs and the consequent high relative humidity of the atmosphere. Most species appear to do best in a humid or a moderately humid atmosphere.

In seeding and planting operations in arid and semi-arid regions, or

in regions having a relatively low degree of atmospheric humidity, emphasis should be placed on the importance of selecting species having well-developed structures to resist the loss of water through transpiration. In regions where the amount of soil moisture is very limited, if fogs are frequent and relative humidity consequently high, many species can be successfully grown. On the other hand, an annual precipitation of 20 or more inches will maintain a forest only of the most xerophilous type in the extremely dry air of southern Arizona, except in the high mountains where the air is more humid.

8. EVAPORATION

Within certain limits the combined effect of atmospheric humidity, atmospheric pressure, temperature, solar radiation, and wind is indicated by evaporation. It is impossible to determine the transpirational water loss of trees directly from evaporation, although in some trees the transpiration and evaporation trends are comparable. Different trees, owing to differences in stomatal movement, cell-sap density, colloidal content of cells, and incipient drying, respond differently to the environmental factors controlling evaporation. However, because of the intimate relation shown by Maximov (1929) to exist between transpiration and evaporation, measurements of both transpiration and precipitation will be very helpful in gaining an understanding of the water relations of forest trees.

The evaporation rate has a marked influence not only on transpirational water loss from trees but also on reduction of water content of the soil, especially in dry regions. Evaporation markedly determines the efficiency of rainfall, especially where the annual precipitation is less than 30 inches (Weaver and Clements, 1938). Many investigations in this and other countries have shown clearly the importance of evaporation in the ecological differentiation of forest communities (Braun-Blanquet, 1932).

9. RATIO OF PRECIPITATION TO EVAPORATION

The ratio of precipitation to evaporation, first introduced by Transeau (1905) is the nearest approach that has yet been tried toward an index of the external moisture relations of plants. From a detailed study of this ratio for such evaporation data as were then available, Livingston and Shreve (1921) concluded that it affords a climatic index by means of which the zonation of the United States with reference to moisture conditions may be clearly shown and that it will be more thoroughly

appreciated as more evaporation data become available. They found that such a climatic zonation is closely paralleled by certain prominent features of the zonation of vegetation types, leaving little doubt that the division of the country into moisture-ratio provinces will be of great value in correlating the distribution of forests with climate.

10. THE PRECIPITATION-VAPOR PRESSURE DEFICIT QUOTIENT

The quotient obtained by dividing the amount of precipitation by the saturation deficit (Niederschlag und Sättingungsdefizit), as proposed by Meyer (1926), has the advantage of the abundant records of air humidity. It appears to give significant results and the larger distributional features of vegetation agree with those of the climatic soil types shown graphically by Jenny (1930). Even more significant results should be obtained by using, instead of saturation deficits, vapor pressure deficits in inches of mercury, because they vary with temperature even when saturation deficits remain constant.

CHAPTER V

CLIMATE

Climate may be defined as the average weather conditions prevalent in any locality. Reliable records of weather continued for many years give climatic averages. Climate is not concerned with the meteorological processes taking place at any one time but rather with the integrated or average effect of these processes over long periods of time. The meteorological processes include the heating, cooling, rising, falling, and horizontal movement of enormous masses of air, the evaporation and condensation of great amounts of water, besides solar radiation and electrical phenomena (Piston, 1931). The climate of any locality is governed by these main factors:

1. The latitude of the locality.
2. Location relative to its position on the continent and to large masses of water — oceans, seas, and lakes.
3. Geographic and topographic conditions, both local and on the surrounding land mass or continent. These factors combine to influence the properties of the various masses of air that pass over a locality and hence the various weather conditions to which it is subjected.

1. IMPORTANCE OF CLIMATE AND WEATHER IN FORESTRY

Climatology is not merely confined to a statistical analysis of climate; is also concerned with the explanation of climatic characteristics of different regions of the earth in the light of meteorological principles and as elements in the natural environment of life. Ever since Humboldt (1805) stressed climate as a causative factor in relation to the development and distribution of vegetation, it has received increasing attention by ecologists and foresters. Various climatic factors have been correlated with the latitudinal and altitudinal limits of forest-tree species and forest vegetation, with tree growth, and with forest soils.

A knowledge of weather is of utmost value in connection with fire control and many other forestry operations such as nursery activities, forest planting, and timber harvesting. Detailed records of air temperature and movement, relative humidity, precipitation, and storm

movements are collected and compiled, and weather forecasts are issued by the United States and Canadian weather services. The United States Weather Bureau issues special forest-fire weather forecasts during periods when the weather is favorable for serious forest fires.

2. WEATHER

Weather is the result of the meteorological processes or the interplay of the physical properties of the air at a specified time. Studies have shown that the physical properties of the air are often nearly the same over hundreds of miles of the earth's surface. Such a large uniform body of air is called an *air mass.*

The earth's atmosphere consists of numerous air masses, each with its own set of physical properties similar within it, but strikingly different from those of adjacent, large air masses. Rapid, abrupt changes in the weather at a locality are produced by the difference in the physical properties of adjacent air masses as they pass over the locality. The most important physical properties of an air mass are temperature and humidity.

3. Sources of Air Masses

Air masses arise at points on the earth's surface where air tends to stagnate and, if the surface is homogeneous, the air masses take on the characteristics of the earth beneath. They are of two main types: the tropical air masses which originate in the tropical and subtropical regions, and the polar air masses which arise in the arctic and subarctic regions. Since the conditions for stagnation of air are not present as a rule in the middle latitudes they are not major sources for the formation of air masses. Each of these types is again subdivided according to the character of the earth's surface at the source region. If formed over water they are maritime air masses; if formed over land they become continental air masses.

4. Characteristics of Air Masses

Air masses are generally circular in shape and are piled up to great heights resembling a giant dome. As an air mass leaves its source region it begins to rotate, and gradually undergoes a continuous change in its properties. Tropical air masses moving toward higher latitudes come gradually in contact with cooler parts of the earth's surface and in cooling lose water vapor by condensation. Polar air

masses advancing over warmer ground are heated from below and gain water vapor by evaporation.

5. Highs and Lows. — Because they are created in regions of stagnation, air masses tend to exhibit relatively high pressures. A *high-pressure system* is an air mass, the rotation around which is outward-moving and clockwise in the northern hemisphere, and which is technically termed an *anticyclone*. A *low-pressure system* is a mixture of air masses, the rotation around which moves toward the center and counterclockwise in the northern hemisphere, and which is termed a *cyclone* or *depression*. The term " cyclone " should not be applied, as it sometimes is by laymen, to sudden violent windstorms which are properly called *tornadoes*.

" Highs " and " lows " are shortened terms applied to high-pressure systems and low-pressure systems, respectively.

6. Air Masses of the United States

All important air masses which pass over the United States originate outside the country. In general, three main source regions supply specific types of air masses destined to control the weather of the United States:

1. Northwestern Canada is the source for continental polar air masses that move across Canada and enter the United States somewhere between the eastern slopes of the Rocky Mountains and the Great Lakes. These air masses are cold and dry and move southeastward, gradually recurving to the east and passing off the Atlantic Coast in the vicinity of Virginia and North Carolina. During the months of June, July, and August these air masses generally do not enter the United States but move eastward from their source. These continental polar air masses are high-pressure systems that are responsible for the " cold waves " in the United States and Canada.

2. The Pacific Ocean is the source for both polar and tropical maritime air masses that move eastward toward the Pacific Coast of the United States and Canada. Only rarely do the polar air masses pass down far enough to reach the Pacific Coast of the United States; hence the mild climate of California and the Pacific Northwest states. The maritime tropical air masses move inland over the mountains of the Pacific Coast states, rise orographically, and deposit heavy precipitation on the windward slopes of these mountains. By the time these air masses reach the leeward side of the mountains most of the moisture has been lost.

3. The Gulf of Mexico and the mid-Atlantic Ocean are the source of tropical maritime air masses that enter the United States along the Gulf of Mexico. They are warm and humid and move northeastward across the eastern United States, passing off the Atlantic Coast in the vicinity of New Jersey. During the winter months these air masses seldom get farther north than South Carolina. In the summer they often reach south central and southeastern Canada.

7. Fronts

A *weather front* is the intersection between two different air masses and the earth's surface. This dividing line between air masses of different physical properties is called a *front*, by analogy with the fighting fronts dividing warring nations. The term is appropriate because weather conditions are often disturbed at a front as if the confronting air masses were at war.

The different fronts commonly recognized by the United States Weather Bureau are defined as follows:

A *cold front* is a boundary line between dry cold air and a mass of humid warmer air, under which the colder air pushes like a wedge, usually advancing southward and eastward.

A *warm front* is a boundary between warm air and a retreating wedge of colder air over which the warm air is forced as it advances, usually northward and eastward.

A *stationary front* is an air mass boundary which shows little or no movement.

An *occluded front* is a line along which warm air has been lifted from the earth's surface by the action of the opposing wedges of cold air. This lifting of the warm air often causes precipitation along the front.

The importance of fronts is easily understood when the energy of storms is considered. Along fronts, tremendous amounts of potential energy (manifested by temperature differences) are concentrated, and this potential energy is used by the air to create kinetic energy. This explains why storms develop along fronts and feed on the potential energy that is accumulated there.

When two air masses of appreciably different densities are brought together, the warmer, lighter air mass tends to flow up over the colder, heavier air mass. In so doing it cools to a temperature below its dew-point. This cooling results in the formation of clouds and precipitation. Thus, frontal zones almost invariably result in stormy weather.

8. Precipitation

The condensation of atmospheric water vapor to form clouds and precipitation is brought about through a reduction of the temperature to a point at which the saturation pressure of the water vapor is less than the existing vapor pressure. Condensation in the atmosphere may be brought about in four ways, which in the order of increasing importance are:

1. The mixing of two unsaturated masses of air having different temperatures and moisture contents.
2. Cooling through direct loss of heat by conduction.
3. Cooling through direct loss of heat by radiation.
4. Cooling due to adiabatic expansion accompanying upward vertical motion. By adiabatic expansion is meant the changing of pressure and density of an air mass where no heat can be communicated to it or withdrawn from it.

Cooling of a body of air by radiation, by conduction, and by mixing with a cooler body of air ordinarily cannot produce appreciable amounts of precipitation. Precipitation resulting from these processes takes the form of drizzle when it occurs in the liquid state. In the solid state it manifests itself as snow grains or ice crystals.

Cooling due to adiabatic expansion accounts for all but a very small fraction of the total rainfall of the world. In this category belong:

1. *Thunderstorm precipitation*. Although thunderstorms can, and often do, develop along a front, the majority of them develop within an air mass. Normally, they occur when an air mass is heated sufficiently from below (by long wave radiation from the earth's surface) to cause considerable instability within the air mass. Consequently, tremendous up and down air currents are set up which transport warm, moist air to great heights, thereby causing condensation, which results in heavy rainfall and sometimes hail.

2. *Orographic precipitation.* Precipitation resulting from forced ascent of air over mountains is called orographic precipitation. The windward sides of mountains receive much of this type of precipitation.

3. *Frontal precipitation.* This type of precipitation is formed when the interaction of two air masses of different physical properties results in a lifting of the warmer, lighter air mass to the condensation level. It makes up most of the winter precipitation of the United States.

9. Storm Paths

During the winter months much of the United States is affected by storms that move in fairly definite courses, tracks, or paths. Cold air

masses from Canada move down across the United States, and along the leading boundaries of these high-pressure systems cold fronts form. As the cold air moves southward, it contacts warm air and showery precipitation results. When these cold air masses reach the southern states they begin to slow down, and low-pressure areas form along the cold fronts. These low-pressure areas form anywhere from Texas to Florida. They then move northeastward, increasing in intensity and causing widespread precipitation. Often they move up the Atlantic Coast. In like manner, low-pressure areas form along the Pacific Ocean cold fronts and move eastward to the Pacific Coast states.

During August, September, and October tropical hurricanes develop over the Caribbean Sea and move northward. Many of these storms pass along the eastern coast of the United States and bring very high winds and heavy precipitation to the Atlantic states.

10. PERIODICITY IN CLIMATE

The climate of the earth is very variable. This variability is made up partly of a long, slow tendency in one direction and partly of innumerable cycles of every conceivable duration from days, or even hours, up to millions of years (Huntington and Visher, 1922). Various hypotheses as to types of climatic change have been developed, such as those of geologic oscillations, glacial fluctuations, sunspot cycles, seasonal alterations, cyclonic vacillations, and daily vibrations. Approximately a 33-year periodicity has been suggested by Brückner (1890). He showed that the chief reason why data drawn from historical sources are unreliable is found in the periodical oscillations in climate. More recently Douglass (1928), in studying the growth rate of trees, suggests that in general the nature of 34- or 35-year periods seems to approach that of the 10.5- to 11-year sunspot cycle on the one hand and of historic pulsations on the other. The cycle found in the growth of the western pines emphasizes the approximate simple fractions of 34 or 35 years, with 11 and 14 years dominating on the coast, 14 and 21 years in Arizona, and 10 and 11 (or 23) in the Rocky Mountains. An 11-year cycle appeared in the long growth records of Sequoia. He found a correlation between growth maxima and sunspot minima. Apparently drought is related to sunspot numbers, for when the relative numbers exceeded 80, rainfall records for the western United States showed a subsequent drought period of 2 or more years.

Oscillations in temperature and precipitation, according to Huntington (1914), occur over the entire earth at average intervals of 35 years as shown below:

Wet Periods	Dry Periods
1691–1715	1716–1735
1736–1755	1756–1770
1771–1780	1781–1805
1806–1825	1826–1840
1841–1855	1856–1870
1871–1885	

Cold Periods	Warm Periods
1731–1745	1746–1755
1756–1790	1791–1805
1806–1820	1821–1835
1836–1850	1851–1870
1871–1885	

The periodicity in climate has a significant effect upon forest vegetation. The longer, more pronounced oscillations, particularly in precipitation, may cause far-reaching changes in a forest. Species normally unsuited to the site may become established during wet or warm periods only to perish during dry or cold cycles. Droughts or cold periods may occasionally be so severe as to cause death of trees or even preclude the reproduction of species normally considered as adapted to the site (Hursh and Haasis, 1931).

11. CLIMATIC PROVINCES

Because of the physiography and the great latitudinal and longitudinal extent of the United States its climate is so varied as to require subdivision. Basing his classification on storm paths and movements, on local and characteristic weather distribution around lows and highs, on cyclonic and anticyclonic winds, and on the general similarity of weather types over each province, Ward (1925) has recognized the following climatic provinces in the United States: (1) eastern, (2) gulf, (3) northern plains, (4) southern plains, (5) northern plateau, (6) southern plateau, (7) northern Pacific, and (8) southern Pacific. Each climatic province contains one or more rainfall types, depending upon the seasonal distribution of precipitation. The importance of the seasonal distribution of rainfall has already been mentioned in Chapter IV and will receive further attention in Chapter XVII.

12. INTEGRATION OF CLIMATIC FACTORS

From the foregoing discussion it is evident that, although each group of factors may be considered separately, the whole aggregation must be considered in arriving at the effect of climate upon forest vegetation.

In nature single factors do not act alone, but in conjunction with the whole complex of factors. The individual factors have many varying interrelations but in the final analysis the significance of each factor depends upon the integrated influence of all factors. This is especially emphasized when efforts are made to determine the relative significance of the various components of climate in influencing origin, behavior, growth, development, structure, occurrence, and distribution of forest vegetation.

Precise measurements of the various climatic components provide the basis for determining the ratio between the various factors, acting either as stimuli or retardants, and the resulting reaction in individual plants, and consequently in the vegetation. Thus, while the intensities of various climatic factors are determined with instruments, the changes that are produced in the vegetation must be determined by observing the effects upon the plants themselves.

For these reasons plants are often grown for a time in the several environments to be compared. Several such plants, known as *phytometers*, are used in each habitat the better to express the climatic factors of an environment in terms of resulting functional and structural adjustments within the plants. Bates and Zon (1922) emphasize the importance of accurate phenological observations in determining the correlation between growth and climatic conditions. *Phenology* is really ecology as applied to the relations between climate and the functions and reactions of plants and animals which are more or less regularly periodic or seasonal in character. It attempts a correlation between integrated climatic factors and biological phenomena.

Pearson (1931) concludes from intensive experiments that the natural occurrence of all species of forest trees in the Southwest very nearly marks their possible range. He also emphasizes the interdependence of significant factors and points out that consequently the lines of demarcation in the characteristics of forests and in the climatic requirements of trees can not be drawn precisely. For example, the efficiency of precipitation depends upon a number of other factors such as temperature, evaporation, and soil properties. Thornthwaite (1931), in proposing a new classification of climates of North America, emphasizes the desirability of using a composite basis consisting of the two most significant climatic elements, seasonal precipitation effectiveness and temperature efficiency. He shows that the relative importance of each depends upon the significance of its effect, that is, where temperature efficiency is adequate, variations in precipitation effectiveness establish the primary climatic boundaries.

Of the various meteorological factors and weather components involved in the climate of a locality, the most important are solar radiation, air temperature, and atmospheric moisture, the latter including atmospheric humidity, precipitation, and evaporation. These factors have been treated in Chapters II, III, and IV. Other climatic factors which at times may have a significant influence upon forest vegetation are: (1) wind, (2) lightning, (3) carbon dioxide content of forest air, and (4) atmospheric impurities.

13. WIND

Wind exerts an influence upon both the form of trees and their distribution. The direct influence is due to its mechanical action. Wind indirectly affects trees through its influence on humidity of the air in immediate contact with them, upon soil moisture and evaporation, and upon transpiration. It profoundly affects pollination and seed distribution. Wind very largely determines the distribution of atmospheric precipitation and in this way indirectly affects forest vegetation.

14. Direct Action of Wind on Forest Vegetation

When wind is strong and blows from one direction, it influences the form of trees and in fact the whole character of the landscape. Warming (1909) states that under its influence trees display the following peculiarities in shape:

1. They are low in stature.
2. The boles are often bent in the direction away from which the prevailing wind blows, and the boughs are curved and bent in the same direction.
3. The branches are short, often irregularly branched and interlaced.
4. The branches are often killed on the windward side, and sometimes one finds new branches and fresh leaves only on the lee side.
5. The crowns often assume peculiar shapes, owing to unilateral branching. As they incline from the windward side they often appear as if clipped and rounded off and expose a very close-set surface.
6. The entire stand inclines in like manner away from the windward side.
7. Sometimes on the most exposed side the branches springing from the roots or from the base of the boles are the only ones to maintain a fair existence. On the windward side a forest may dwindle to scrub and this in turn may be resolved into scattered, or isolated, cushion-like individuals.
8. The leaves become smaller than usual and often are more or less brown in patches, or reddish, particularly at the margins.
9. The transverse section of the bole is influenced by the wind. The diameter is greatest in the direction the prevailing winds blow.
10. The height growth in individual trees in stands is limited to the general canopy level.

Wind is also an important factor in determining the position of timberline on high mountains, as is well illustrated in the timberline on the west sides of the San Francisco Mountain peaks in northern Arizona.

15. Effect of Continuous Stress Caused by Wind

The continuous stress occasioned by constant winds results in an increase in mechanical tissues of a tree where stresses occur and consequently a tree is better fitted to resist mechanical injury. Species indigenous to windy regions not only develop in a manner which better enables them to resist wind, but they are better fitted to survive marked deviations from the normal shape which they are forced to assume. In such regions branches and boles are more or less conspicuously bent away from the normal direction of growth. The mechanical effect of constant high winds is often so great in prairie regions, along coasts and on mountains, that windbreaks of resistant species must be developed before trees can be successfully introduced that are accustomed to sites where a calm condition of the atmosphere usually prevails.

Exposed situations are usually characterized by trees of abnormal form due to the direct impact of high, constant winds. Trees at the sea shore not only bend away from the direction of prevailing winds, but branches on the windward side are often killed, partly by the direct impact of the wind, partly through its desiccating influence, and partly through the abrasive action of wind-carried sand and snow. Tall trees, standing over an understory of shorter trees, usually point their crowns or actually lean away from the direction of the prevailing wind. This condition is very pronounced in the virgin stands of pine and mixed hardwoods in the Adirondack Mountains where white pine rises above the other species. On exposed mountains at very high elevations, where wind velocity is great, trees are low and scrubby. They often grow as dwarfs, with tops flat and uniform in height, as if artificially trimmed. Some take a prostrate form, creeping along the ground and erecting only a short head as a crown. Pitch pine on the coast often assumes a prostrate form. Plants grown under artificial wind having velocities of 10 to 15 miles per hour show the gnarled and twisted appearance characteristic of trees growing in windy situations (Martin and Clements, 1935).

16. Windfall and Windbreak

Velocity of the wind in all habitats varies between wide limits, from a perfectly calm condition to that of more or less violent storms. The

mean wind velocity of different habitats also varies between wide limits. The occasional high winds of all regions cause windfall and windbreak (Fürst, 1893). This type of mechanical injury, however, is most common in regions which usually experience a calm atmosphere. Here forest vegetation does not become adjusted to withstand great wind pressure and as a consequence occasional severe storms often cause great damage. In regions where the mean velocity of wind is high, as on islands, along coasts, on exposed mountains, and in most prairie regions, trees become adjusted to wind action and are able to resist damage. Trees are influenced much more by wind than is the lesser vegetation because of a marked increase in velocity of the wind with height above ground.

In the mountains of Europe, the location of cuttings is often made chiefly with reference to possible damage by windfall, and one of the considerations in planning the ultimate development of a forest is to arrange the stands of different ages so that the mature timber may be cut without damage from windfall. The kind of reproduction cutting is determined by the likelihood of windfall. In many places a particular system of cutting can not be practiced. Thus in a pure spruce forest on an exposed slope, the timber can not be thinned excessively because the remaining trees are likely to blow over. A clear-cutting system must generally be used.

The greatest danger from windfall arises under the following conditions:

1. When stands are grown in situations exposed to high winds, like ridges and slopes with an aspect toward the prevailing wind. High slopes often have even-aged stands upon them because of their development after windfall.

2. When stands are grown on shallow soil and on heavy, clay soils. Windfall is frequent on soil into which roots cannot penetrate deeply enough to gain a firm foothold. Exposed situations often have thin soil, which adds to the danger of windfall.

3. When stands are grown in swamps and on other wet soils. Trees in swamps are likely to be thrown by wind, partly because the soil is soft and does not offer a firm support for trees, and partly because the root systems of the trees are near the surface. On ordinary soils the influence of water in loosening the soil is seen in the increased damage from windfall in wet seasons.

4. When stands are grown in regions frequented by severe storms, tornadoes, and hurricanes.

5. When a stand is composed of trees having shallow root systems, such as spruce and fir as compared with oak and hickory.

6. When a stand is composed of conifers. Most conifers hold their foliage throughout the year and present a large surface to the wind at seasons which are characterized by highest winds. They usually have long, slender boles and many of them have shallow roots.

7. When dense stands are opened by thinnings. Trees in dense stands develop long, slender boles, short, narrow crowns, and narrow root systems. They rely on the mutual support of their neighbors for wind resistance. When such stands are opened by thinnings, the danger from windfall is very great except with the most windfirm species.

8. When a stand is near the summit of a ridge on the windward side.

9. On the leeward side of a ridge the wind sweeps over the ridge and strikes the crowns of trees growing just below the summit.

10. When a stand is composed of trees with widespreading, spherical, or broadly ovate crowns. Narrow, conical-crowned trees withstand high winds much better. It is significant that conifers growing on high, exposed sites are of the latter type.

Another cause of damage by wind is actual breakage of the stems or branches. Severe storms, in the nature of tornadoes, break trees at the butt, when deep-rooted and not easily overturned. Usually, however, the boles of trees are not broken unless there is some point of weakness. A bole may be weakened by decay at the heart, caused by disease. Fires often burn partly through a tree at the base leaving it in a weakened condition; thus pine, which has been boxed for turpentine and weakened by fire, is particularly subject to wind breaking. Trees are also weakened by localized diseased spots at some point on the shaft, as illustrated in the canker disease, which is very prevalent in scarlet oak. Crowns of trees are often injured in the winter during ice storms. Breakage is most serious in the top of a tree, which, when coated with ice, is often broken by the wind. This type of injury is illustrated in silver maple, chestnut, and chestnut oak in the hardwood region of New England and in southern New York.

17. Resistance of Different Species to Wind

From the preceding discussion it is evident that different species of trees and different types of vegetation have varying powers for resisting mechanical injury from wind. Of the trees common in southern New England the hardiest in this respect are pitch pine, hemlock, and red cedar among conifers; and willow, hornbeam, and alder, among hardwoods. Among the least resistant are silver maple, boxelder, and ash. The most important protection against wind is natural or artificial protective barriers.

18. Indirect Effect of Wind on Forest Vegetation

To a considerable extent the effect of wind on forest vegetation is due to increased transpiration, leading to desiccation. Wind dries plants so

that they must adapt themselves to existing wind conditions in order to avoid desiccation. In a calm atmosphere the air in contact with a plant becomes humid, so that transpiration is retarded. Even when the atmosphere is humid but the wind high, transpiration is excessive. Owing to the increase in wind velocity with elevation above the surface, short plants are much better protected than taller ones. Damage from the desiccating effect of wind is much increased when the activity of roots is diminished by coldness of soil, when the loss of moisture from the foliage and branches can not be adequately supplied by absorption. Winter-killing of foliage often results from the desiccating action of high winds during periods when the loss of water can not be made up by a supply from the soil. The drying of the soil by wind may result in the exclusion of certain species from sites, where otherwise they would grow. On certain sites in the semi-arid West, areas cleared of forest are reforested with great difficulty by natural or artificial means, owing to the drying action of wind. The growth of trees and the final yield of a forest may be seriously affected through the drying action by wind. In cutting a forest, foresters have constantly to guard against exposure of the soil which results in its deterioration. This is particularly true on exposed slopes.

19. Effect of Wind on Distribution of Forests

Although the absence of trees from many places is due to wind, in most places where trees do not grow naturally their absence is due to cold, insufficient soil moisture, and other causes aside from wind. Wind in particular marks the boundaries of forests in polar regions and on high mountains (Humphreys, 1916). Forests usually cease where the mountain breaks up into isolated peaks. Above this point forests occur where there is local shelter from wind and where the soil is deeper and moister. It is in valleys sheltered from wind that forests extend farthest into arctic regions. In high alpine regions the slope facing the prevailing wind is sometimes covered with low, heath-like vegetation while the leeward side is covered with forest.

20. Utility of Wind to Trees

Wind is of importance in a forest in conveying fresh supplies of carbon dioxide to the foliage (Schimper, 1903); in the transport of pollen of many species that are aided by wind in the pollination of anemophilous flowers; and in the dissemination of seeds. Wind pollination is most common in species which naturally grow in exposed places where the air

is usually in motion. It is seldom found in species that grow in the interior of a forest where the air is usually calm.

The work of wind in seed dispersal is of the utmost importance in forest distribution. The distance that seeds are carried by wind depends on the tree height, the velocity of wind during seed dispersal, and the rate at which seeds fall through still air. With a knowledge of these conditions it is possible to determine the probable distance to which seed will be carried. The number of feet seed will be carried horizontally equals the number of seconds required for the fall of the seed from its place on the tree multiplied by 1.47 times the velocity of the prevailing wind in miles per hour.[1] Siggins (1933) determined experimentally the rate of seed fall in still air for a large number of forest trees. From his work it is evident that small light fruits and seeds with large wings, or other structures that facilitate buoyancy, may be carried many miles by strong winds or from high mountains.

21. LIGHTNING

Lightning exerts a very positive influence upon composition and character of forest growth. This influence is both direct and indirect. There are no available data in this country showing frequency with which our forest trees are struck by lightning. Information is not available as to degree of injury suffered by different species in the same locality or in different localities. European observations show, however, that the damage from this cause, both direct and indirect, is far greater on some sites than on others, and that certain species are more subject to being struck than others (Fürst, 1893). On the whole, forests of mountain regions are more exposed to injury than those at low elevations and on comparatively level land.

Although all trees are more or less subject to this kind of injury, beech appears to suffer but little as compared with oak and chestnut. Conifers, particularly spruce and pine, are frequently struck. On the whole, conifers appear to suffer more from lightning than broadleaved trees. They usually grow on more exposed sites and they do not as readily recover from scoring of the bark and from other mechanical injury. In general trees that have a large amount of moisture present in the wood are more severely injured than species with less moisture. Height, isolation, conductivity of wood, character and spread of foliage, and position of roots, all affect the liability of trees to be struck by lightning.

[1] A wind having a velocity of 1 mile per hour blows 1.47 feet per second.

22. Direct Effect of Lightning on Forests

The direct effect of lightning is chiefly mechanical in its action. A whole tree may be thrown, large limbs broken off, or the bark stripped from one side. Hartig (1889) has shown that trees may be killed outright, without any visible mechanical injury. In such cases the electricity, in passing between the top of a tree and the ground, is carried over the surface of the wet bole, killing the cambium. Recent European observations indicate that stagheadedness, which is frequently seen in alpine forests, often is due to electricity through induction without the tree's being actually struck; the tree conducts the electricity between the atmosphere and the soil below.

The frequency of damage by lightning in any particular region appears to be largely controlled by local topography. Records taken in the western United States clearly indicate localized lightning zones in various mountainous regions (Show and Kotok, 1923; Gisborne, 1926).

When electricity of high voltage is carried on wires not properly insulated, trees coming in contact with them may also be severely damaged. Often the damage to street trees and those growing along country roads is not fully comprehended. Direct current appears to be far more harmful than alternating current. When wires come in contact with trees more or less extensive burns occur, and there is reason to believe that the injury is not wholly local (Stone, 1914).

23. Indirect Effect of Lightning on Forests

The chief indirect effect of lightning is in causing forest fires (Plummer, 1912). In alpine regions lightning is the chief cause of forest fires and all forests are more or less subject to fires caused by it. Where thunder storms are not followed or accompanied by more or less heavy downpours of rain, lightning is the chief cause of forest fires in almost every large forested area.

The only method of measuring the frequency and effect of lightning as a site factor is by direct observation of its occurrence and its influence on vegetation.

It has long been known that rain and snow contain small quantities of fixed nitrogen, a part of which presumably is fixed by electrical processes occurring in the air. Curtis (1932) points out that, although the natural fixation processes in the atmosphere are responsible at most only for the nitrite and nitrate nitrogen, even this may have been formed by oxidizing ammonia derived from the disintegration of nitrog-

enous organic matter, but "there is certainly some nitric oxide formed along the path of a lightning flash, and this may be the source of the oxidized nitrogen present in rain. Whatever the origin of the fixed nitrogen in rain and snow, the soil is benefited by the nitrogen so received."

24. CARBON DIOXIDE CONTENT OF FOREST AIR

Carbon dioxide, one of the two raw materials essential to photosynthesis, is obtained naturally by plants from both soil and air. The absorption from the atmosphere of carbon — one of the main components of all organic materials — is important in the exchange of gases between plants and the air. Forests assimilate large amounts of carbon dioxide. Although the amount of CO_2 in ordinary air is only about 3 parts in 10,000, its concentration in the lower layers of atmosphere under a forest cover may reach 8 parts in the same volume of air (Braun-Blanquet, 1932). The concentration of CO_2 at night, when assimilation is suspended, is higher than in the daytime (Lundegårdh, 1931). Büsgen and Münch (1931) suggest that the higher production of CO_2 in forests may contribute to the rapid growth of trees in calm, moist situations, where there is little wind movement and a rapid decay of large amounts of litter. The much higher CO_2 content of forest air near the ground may be of considerable importance to vegetation growing just above the forest floor (Meinecke, 1927; Lundegårdh, 1931). It may also contribute to the survival of the undergrowth in forests by compensating for the low light intensity of the forest floor. Gut (1929) has shown that the CO_2 content of air is subject to greater variations in beech than in pine forests, indicating that, while the gas exchange is more active in deciduous forests, their growth rate is slower. However, Baker (1934) concludes that it is unlikely that much increase in growth can be obtained through a direct increase of carbon dioxide content of the air following the rapid decay of large amounts of litter.

25. ATMOSPHERIC IMPURITIES

In the vicinity of volcanoes and hot sulphur springs forests suffer to a greater or less extent from poisonous gases. Sulphurous acid present in the vapor is the chief factor in causing this injury. Because of the very limited areas over the earth's surface where this kind of injury occurs, its discussion as a site factor would scarcely be warranted were it not that the same kind of injury occurs wherever large quantities of

coal are burned, as in the vicinity of smelters (Mason, 1915). The comprehensive researches of Wislicenus and Neger (1914) prove that sulphurous acid is absorbed in gaseous form by the foliage, where it is oxidized into sulphuric acid and acts as a poison. As different species exhibit varying degrees of resistance to atmospheric impurities they should be taken into account when plantations are made near industries that consume large quantities of coal. Ethylene, the most common constituent of coal gas, is very injurious to trees and may even kill them. Although under ordinary forest conditions gases and smoke are usually not present in sufficiently large quantities to kill trees, still in or near large cities or certain industrial developments their influence is often very pronounced.

26. Resistance to Injury from Atmospheric Impurities

Coniferous species are most sensitive to air impurities because of their persistent leaves. The degree of resistance is nearly inversely proportional to the length of time that leaves remain on the trees. Spruce and fir are very sensitive, pine less so, and larch the least sensitive of all conifers (Hartig, 1889). In broadleaved species, oak and chestnut are among the least sensitive, maple, ash, and elm are more so, and beech, poplar, and cherry are very sensitive. Relative humidity of the atmosphere very materially influences the degree of injury. All species are much more sensitive to injury in a damp, foggy atmosphere.

CHAPTER VI

SOIL CONDITIONS

The soil is a natural body that covers most of the land surface of the earth, differentiated into horizons of mineral and organic constituents, usually unconsolidated and of variable depth. It differs from the parent material below in morphology, composition, physical and chemical properties, and biological characteristics.

1. SOIL IN RELATION TO TREES

Trees and other plants whose roots penetrate the soil obtain water and nutrients necessary for the physiological processes associated with growth. The soil provides the trees and lesser vegetation with space for root growth and development. The nature of the soil and parent material determines not only the kind, but to a considerable extent the distribution of vegetation. Seeds germinate on or in the soil. Roots push their way between soil particles, absorbing water and nutrients; if the character of the soil is such that roots can not grow in it or if there is not an adequate supply of water and nutrients, obviously trees will be unable to grow.

Although climate is most important in determining the range of a species, the condition of the soil often is responsible for limiting its occurrence. Deficiency in precipitation may result in a soil's becoming too dry for a given species to grow well or even to reproduce.

Since the soil provides water and nutrients for trees, there is scarcely a physiological process that is not controlled by it or a silvical characteristic that is not dependent upon it. Rate of growth, yield, longevity, form, quality of wood, tolerance, and reproduction are all influenced and may be modified in one way or another by the soil. Trees obtain carbon dioxide from the air and water and nutrients from the soil for food synthesis.

The influence of soil is apparent in the local distribution of trees. It is well known that within its geographical range the occurrence of a species is more or less localized, and it is only on certain sites that a particular species occurs. The quality of a site is determined by many factors, but they can usually be summed up in character of the soil and its topographic position, if climatic conditions are similar.

The physical, chemical, and biological relations of the soil to forest

vegetation are extremely complex. The soil alone is a very complex entity, physically, chemically, and biologically. The effect of soil properties on the growth of forests is often difficult to study because of the great length of time necessary to grow most trees to maturity. The singularity of forest-soil problems is particularly apparent when compared with those involving the effects of soil properties on the yield of other crops such as wheat and corn, in which results may be obtained in one or, at most, a few growing seasons.

2. THE SOIL PROFILE

The soil profile is composed of various horizons which are exposed in a vertical cut through the soil from its surface to the parent material. It can usually be subdivided into four broad horizons, the classification being based on the characteristics of the horizons. The term horizon is used instead of layer or stratum because the latter implies definitely delimited planes, while a soil horizon is often irregular and delimited by relatively broad transition zones.

The following horizon designations are in common use:

A_0 Horizon: The layers of unincorporated organic débris upon the surface of the mineral soil.

A Horizon: The upper layers of the soil mass, or the eluvial horizon, from which, in the process of soil formation, material has been removed in suspension or in solution.

B Horizon: The layers of deposition, usually immediately beneath the *A* horizon, into which in the process of soil formation material has been carried. The horizon of illuviation.

C Horizon: The layers of relatively unweathered parent material in which the processes of eluviation and illuviation have not been active.

Each horizon, *A*, *B*, and *C*, may be subdivided into two or more subhorizons and designated by numbers, that is, A_1, A_2, B_1, B_2, B_3, C_1, C_2. The A_1 horizon is the region of incorporated organic matter. It is usually distinguished by being darker in color than the remainder of the *A* horizon.

Soil is not a geologic formation, but rather the weathered product of a geologic formation — the parent material. All processes involved in the formation of soil material from rock are also active in the development of a soil, but, in addition, other processes are active in soil development which are not an essential part in the formation of soil material.

Rock as a geological body is broken down by weathering and the product is acted upon by processes of soil development. Weathering as a geological process and the processes of soil development usually

6. Laterization

In this process of soil development, which is dominant in tropical and equatorial climates, silica, alkalies, and alkaline earths are removed

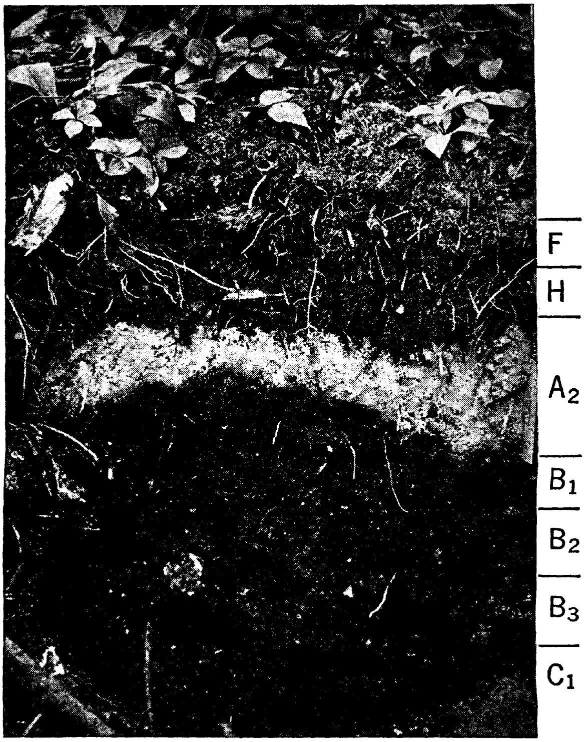


FIG. 6. — Profile of strongly podsolized, brown forest soil. Cherry Mountain, New Hampshire. (*Photograph by M. F. Morgan; from Lunt, 1932.*)

from the surface soil, and iron and alumina accumulate by residual action. Laterization takes place under conditions of alkaline hydrolysis. In the humid tropics the decomposition products of organic matter are not highly acid, and conditions are favorable for the solution of silica, alkalies, and alkaline earths, much of which are removed in the drainage waters.

7. Calcification

This process is not restricted to one group of soils but is universal (Marbut, 1928). However, it is important in soils developed under conditions of rainfall and temperature that result in a permanently dry layer or area in the soil profile and in the soil material between the water table and the zone of maximum penetration of rain water. Such a permanently dry zone is usually found in regions where the annual

FIG. 7.— Profile of non-podsolized, brown forest soil. Yale Forest, Keene, New Hampshire. (*Photograph by H. J. Lutz.*)

rainfall is less than 20 inches. The carbonates which have been produced through carbonation of the material in the upper moist zone are carried down through solution to the top of the dry zone and are deposited there when the water evaporates. Carbonates that are present in the soil material before the soil process becomes active are carried down and deposited in a like manner. There is also an accumulation of sulphates at some places, usually below the zone of carbonate accumulation.

The soil solution is alkaline during the early part of the calcification process. When the surface of these soils becomes sufficiently leached,

under conditions of moderate rainfall, the acid organic matter which accumulates on the surface promotes the podsolic process. A forest cover hastens the beginning of the podsolic process, but soils which accumulate carbonates in the temperate zone do not ordinarily have a forest cover.

8. SOIL CLASSIFICATION

Many categories have been proposed for the classification of plants and animals based on morphology, color, habits, size, food, and manner of reproduction as well as external factors of environment, such as habitat, origin, geographic distribution, and economic use. However, in the systems that prevail in all natural sciences the objects of classification are grouped solely on the basis of their important characters or properties.

Probably the most primitive of all soil classifications was based on productivity. It is the natural viewpoint of agronomists. The geological viewpoint was dominant early in the history of soil classification. Soils were classified on the basis of the composition and lithological nature of the accumulated or deposited soil material or parent rock. Little attention was given to the features of the profile developed by the soil-forming processes. Fallou (1862) differentiated soils into residual and alluvial. Dokuchaev (1879) considered the effect of climate on the soil and published a classification based upon the fundamental characteristics of the soil itself as far as they were known.

The great importance of moisture and temperature in soil formation was recognized by Sibirtzev (1900) who suggested a zonal classification of the soils of Russia. Glinka (1927) offered a classification of soils based on the processes and dominating factors in their development. His system is essentially climatic in nature.

The United States Soil Survey classifies and maps soils on the basis of profile characteristics, and not on the basis of the supposed or partly proved causes which have produced the characteristics. Marbut (1928) was the chief exponent of this system.

Marbut (1935) classified the soils of the United States on the basis of mature profiles as follows:

Category VI	Pedalfers (VI-1)	Pedocals (VI-2)
Category V....	Soils from mechanically comminuted (pulverized) materials. Soils from siallitic (acid) decomposition products. Soils from allitic (laterite) decomposition products.	Soils from mechanically comminuted (pulverized) materials.
Category IV....	Tundra Podsols Gray-brown podsolic soils Red soils Yellow soils Prairie soils Lateritic soils Laterite soils	Chernozems Dark-brown soils Brown soils Gray soils Pedocalic soils of arctic and tropical regions
Category III...	Groups of mature but related soil series Swamp soils Glei soils Rendzinas Alluvial soils Immature soils on slopes Salty soils Alkali soils Peat soils	Groups of mature but related soil series Swamp soils Glei soils Rendzinas Alluvial soils Immature soils on slopes Salty soils Alkali soils Peat soils
Category II....	Soil series	Soil series
Category I.....	Soil units, or types	Soil units, or types

The Pedalfers include those soils in whose maturely developed profile no higher percentage of lime carbonate is found than in the parent material beneath them and in which either a shifting or an accumulation of sesquioxides, and often both, has taken place. The Pedocals include those soils in which lime carbonate is found in some horizon, of a fully developed profile, in higher percentage than in the parent material. The Pedalfers are forest soils; the Pedocals are grassland and desert soils.

Category V differentiates soils on the basis of the origin of the colloidal fraction into three broad classes; that is, mechanically pulverized material, acid decomposition products, and decomposition products of laterization or of laterite rock.

In Category IV the soils are subdivided into broad environments, or great soil groups. The groups are essentially climatic and the profile characteristics that are typical of each are most closely correlated with temperature differences in the Pedalfers and with rainfall differences in the Pedocals.

Category III includes groups, the units in each of which have features in common that are a result of local environmental conditions, such as topography or unusual characteristics of parent material.

The soil series groups compose Category II. The soils in a series are similar in profile characteristics excluding texture of the *A* horizon, have the same general conditions of relief and drainage, and usually have a common mode of formation.

Category I, the ultimate unit or soil type, differentiates soils on the basis of texture of the *A* horizon. A soil type consists of a soil which, throughout the extent of its occurrence, has a relatively uniform texture of the *A* horizon and relatively uniform profile characteristics.

9. PHYSICAL NATURE OF SOIL

The physical properties of soils are of great importance to tree growth because of their effect on the supply of water and nutrients. The soil is composed of material varying in size from boulders to minute particles of colloidal size. The percentages of the various size classes of particles give to the soil most of its properties as a physical system. The amount of the various fractions (particle diameter classes) in a soil is determined by mechanical analysis. The various size classes of mineral particles under 2 mm. in diameter recognized by the U. S. Bureau of Chemistry and Soils (Olmstead, Alexander, and Middleton, 1930) are:

Name of Fraction	Diameter Size Classes — Millimeters
Fine gravel	2.0 to 1.0
Coarse sand	1.0 to 0.5
Medium sand	0.5 to 0.25
Fine sand	0.25 to 0.10
Very fine sand	0.10 to 0.05
Silt	0.05 to 0.005
Clay	<0.005
Colloid	<0.002

Bouyoucos (1927, 1928, 1930) has developed a hydrometer method of mechanical analysis that is quite rapid and gives good results with most soils. The size classes of soil particles measured by this method are:

NAME OF FRACTION	DIAMETER SIZE CLASSES — MILLIMETERS
Total sands	2.0 to 0.05
" Total colloidal content "	Part of the silt and all of the finer fractions
Silt	0.05 to 0.005
Clay	<0.005
Fine clay	<0.002

The textural grade of a soil can easily be determined if the percentages of sand, silt, and clay are known (Fig. 8). The mineral part of soil is composed of particles of almost infinite number of sizes and shapes. Mechanical analysis data give the percentage of particles within certain size classes. Material above 2.0 mm. in diameter is considered gravel if it is rounded and stone if it is not rounded. The material larger than clay size — silt, sand, gravel, and stone — forms the physical framework or skeleton of the soil; and the finer fractions — clay and colloidal material — compose what may be called the active part of the physical system, because in them the important phenomena of base exchange and water absorption are centered.

10. SOIL STRUCTURE

An important physical characteristic of soil is its structure, which is determined by the extent and type of aggregation of the particles. Soil structure has a significant effect on erosive properties. Working with Iredell sandy clay loam, an erosive soil, and Davidson clay, a non-erosive soil, Lutz (1934) found that the particles of the Iredell formed " stone-fruit-like " aggregates and Davidson particles formed " pop-corn-ball-like " aggregates. Material of silt size and less was compared. A high percentage of large aggregates in the Davidson soil allows good percolation of water to great depths, although the soil contains a high percentage of clay.

Baver (1934) has classified soil structure and related it to the main soil groups. He defined structure as the arrangement of primary and secondary particles into a more or less definite pattern. The micro-structure apparently markedly influences the macro-structure. With reference to their micro-structure, soils are divided into three main

classes: (1) chiefly secondary particles, (2) chiefly primary particles, and (3) a mixture of primary and secondary particles in which there is a single-grained arrangement with the secondary units. Baver defined granulation as the process of breaking up of soil aggregates into secondary products or units, which are similar in structure to the original aggregates but smaller. Prism-like and plate-like secondary

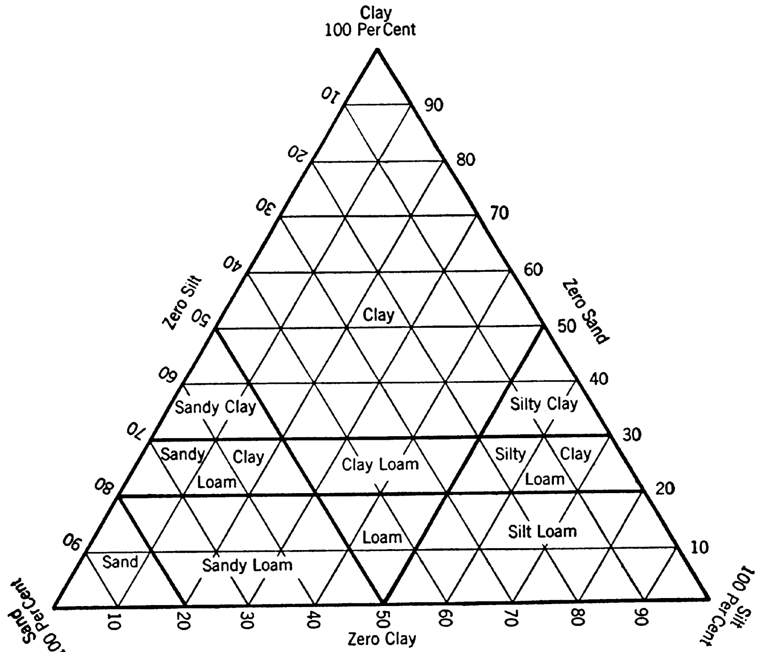
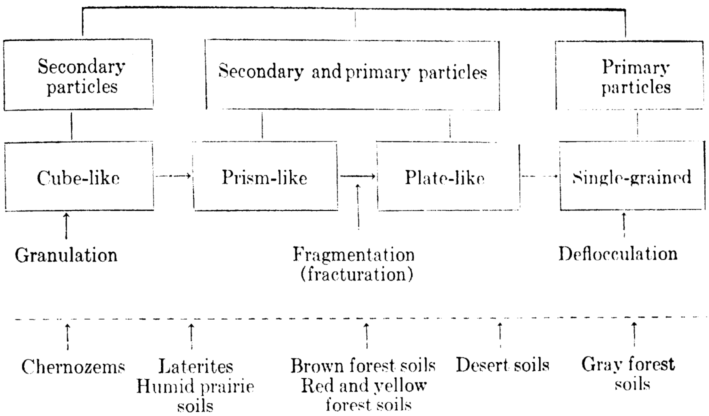


FIG. 8. — Diagram showing 10 of the main soil classes in relation to their percentage composition of sand, silt, and clay. (*After Davis and Bennett, 1927.*)

particles break up along definite cleavage planes. They are angular and non-porous as compared to the true soil granule. Baver classified the types of soil structure as related to the arrangement of primary and secondary particles as follows:

STRUCTURAL ARRANGEMENT CONSISTING OF



The type of soil structure influences water percolation, root penetration, aeration, and erosion.

11. Volume Weight

The true specific gravity of mineral soil varies between 2.6 and 2.7. However, the apparent specific gravity or volume weight may be as high as 1.70 in sands and less than 1.00 in the *A* horizon of well-granulated, heavy-textured forest soils. Organic matter decreases the volume weight and so do the many tunnels of soil animals.

12. Depth of Soil

Depth of the entire soil mass as well as thickness of its various horizons are important in the growth of a forest because of their bearing on the total amount of water stored in the soil and that available for plant growth. In addition the depth and physical character of the various horizons determine to a large extent the growth of tree roots.

13. INORGANIC CHEMICAL NATURE OF SOIL

Total chemical analyses of most rocks that weather to form the inorganic part of soil indicate that they contain all of the elements necessary for tree growth. However, during the processes of soil development many of the important elements such as calcium, magnesium, potassium, and phosphorus are leached from the surface soil, or *A* horizon; but usually a part of the total leached material is precipitated in the *B* horizons or at lower depths and may again be brought to the surface in the periodic litter fall in a forest.

The most important classes of soil-forming minerals are (1) silicates, (2) oxides and hydroxides, (3) carbonates, and (4) phosphates. Of these silicates are by far the most important as they weather to form the finer fractions (silt, clay, and colloidal).[1] The silicates give to the soil calcium, magnesium, sodium, potassium, flourine, iron, aluminum, and silica; the oxides and hydroxides give quartz (SiO_2), which makes up the skeleton of many soils, and manganese, iron, and aluminum; the carbonates supply calcium, magnesium, lead, and copper; and the phosphates contribute calcium, flourine, and phosphorus. Most rocks contain many other minerals of different composition, so that in general the parent rock from which soils are developed contains all the inorganic elements necessary for plant growth. However, exceptions can be found in aeolian and fluvial sands, which may be almost entirely silica and, consequently, quite sterile with regard to the elements essential for plant growth.

14. BASE EXCHANGE

The important chemical reaction known as base exchange is centered in the colloidal fraction (both organic and inorganic) of soil. The colloidal micelle or nucleus is negatively charged and has the power to adsorb cations of calcium, magnesium, potassium, sodium, hydrogen, and other elements. The replacing power of the various cations is a function of the magnitude of their charge and their degree of hydration. Any cation can be replaced by another cation and thus go into solution and be made available for absorption by plant roots. Nitrates are not adsorbed and hence are readily lost from the soil by leaching if they are not immediately used by plants after they are formed by the nitrifying organisms. A soil is said to be saturated when the exchange complex is completely saturated with bases. The degree of unsaturation depends upon the amount of hydrogen ions adsorbed. Calcium ordinarily makes up 80 percent of the exchangeable bases in Pedalfers.

The soil solution contains the same ions that are adsorbed on the surface of the colloidal particles. Ions that are lost from soil by leaching and removal in drainage waters, or by absorption by plant roots, are replaced by the decomposition of soil minerals and the release of new elements that were previously locked up in complex mineral compounds. In addition, many metallic elements and nitrogen are returned to the forest floor in the litter which undergoes decomposition, thus releasing the constituents which return to the soil solution and the exchange complex and are again available for absorption by plant roots.

[1] The chemical composition of soil-forming minerals is discussed by Burt (1927).

15. NATURE OF SOIL ORGANIC MATTER

Soil organic matter may be divided into two broad classes: (1) remains of plants that grow in soil and whose mature products return to it in relatively undecomposed state, such as leaves, twigs, and stems of trees and lesser plants, and their dead roots; (2) living and dead organisms, plants, and animals that reduce and decompose material in class 1.

Humus is that part of the soil organic matter that has reached a stage of decomposition such that its various constituents (leaves, twigs, and other plant remains) cannot be identified by macroscopic methods. The chemical nature of humus varies with the chemical composition of the original organic débris from which it is derived, the environment in which it is formed, the organisms that are responsible for its existence, and its stage of decomposition. Humus may be present on the surface of mineral soil as a continuous or discontinuous layer or may be incorporated into the mineral soil through the activity of soil animals, the action of percolating water, and the death of roots.

The soil organic matter, both on the surface of mineral soil and incorporated in it, is the seat of the very important process of nitrogen mobilization. Through the decomposition of soil organic matter, nitrogen is made available for plant use.

Humus is not a definite substance but a variable complex mixture of the following broad groups of substances (Waksman, 1936):

1. Fats, waxes, and resins, or substances soluble in ether, alcohol, benzol, chloroform, and similar solvents.
2. Carbohydrates and related compounds.
3. Proteins and their derivatives.
4. Lignins and their derivatives.

The fertility of a forest soil depends largely upon the rapidity, type, and extent of decomposition of the organic débris that is added to it. Waksman (1936) lists the following factors as determining the nature and rapidity of decomposition of soil organic matter:

1. Nature of the higher vegetation. Leaves of conifers vary markedly in chemical composition from leaves of hardwood trees; this difference in composition exerts a marked influence upon the type and rapidity of the decomposition processes.
2. Nature of microorganisms active in the disintegration of the residues. When fungi are predominant, a type of humus will result which is different from that produced mainly by bacteria and invertebrates.
3. Nature of the soil, particularly its structure, which affects the penetration of water, and its chemical composition, especially the reaction and abundance of basic materials.
4. Environmental and climatic conditions, including rainfall and temperature. The aerobic or anaerobic nature of the decomposition processes, the preferential

development of fungi or bacteria, and the speed of decomposition are all considerably influenced by environment. Climate and vegetation are the two most important controlling factors which determine the type of forest humus produced.

16. Forest Humus Types

The forest floor[1] or A_0 horizon, under a forest stand old enough to produce sufficient litter to reach a thickness at which a condition of equilibrium between addition and decay obtains, can be subdivided into two or more layers. The uppermost layer is composed of relatively undecomposed, freshly fallen litter and has been designated by the letter *L* (Hesselman, 1926). Beneath the litter layer a well defined layer of actively decomposing organic débris is found, which is usually characterized by an interwoven mass of fungous mycelia, and in which the components (leaves, twigs, and other material) are still distinguishable. This layer has been called the *F* layer. In some soils, particularly those in cool, humid climates supporting a coniferous forest, a more or less continuous layer of material is found beneath the *F* layer in which the original structure of the plant residues can no longer be recognized. It has been called the *H* layer. The *H* layer is also known as the humified or humus layer.

The classical work of Müller (1887) on humus types has had much influence on European silviculture, and also has been the inspiration for work in this country on humus types. He pointed out that the nature of the humus type definitely modified the type of soil formed. He also called attention to the fact that the humus type was determined by vegetation, climate, and moisture conditions, physical and chemical properties, and biological activities in the soil, which lead to specific processes of decomposition by the soil organisms.

Nomenclature for forest humus types has been in a chaotic state. However, it is now generally conceded that two broad classes of humus types exist:

1. *Mull*, in which there is a more or less intimate mixture of the humus proper and the mineral soil. Such a horizon is often designated as A_1 — the horizon of incorporated humus.

2. *Mor*, in which the organic matter or humus proper (*H* layer) is practically unmixed with the mineral soil. The transition to mineral soil is always distinct.

On the premise that definitions of forest humus types, according to Müller (1887), must be based on morphological characters which can be easily observed directly in nature, Bornebusch and Heiberg (1936)

[1] *Forest floor* is the entire accumulation of organic matter on the soil surface.

proposed the following nomenclature, applicable to well-drained forested soils, for the two main types and for suggested examples of subtypes:

1. *Mull:* Mixture of organic matter and mineral soil; crumbly, granular, or compact structure; transition to lower layers not sharp.

a. *Coarse mull:* coarse grain structure; organic matter very conspicuously mixed with mineral soil (usually 5–20 percent organic content, exceptional cases even higher).

b. *Fine mull:* fine grain structure; organic content high (usually over 50 percent).

c. *Firm mull:* dense compact structure; usually low content of organic matter, often less than 5 percent.

2. *Mor:* Organic matter practically unmixed with the mineral soil, usually more or less matted or compacted. Transition to mineral soil always distinct.[1] Often composed of two layers, *F* layer and *H* layer (Hesselman).

a. *Granular mor:* *H* layer pronounced, and fine granular in structure. Lower part somewhat compacted. Under dry conditions very easily broken into fine powder when pressed by hand.

b. *Greasy mor:* *F* layer usually relatively little developed, often more or less fibrous. *H* layer thick, compact, with a distinct greasy feel when wet; hard and brittle when dry.

c. *Fibrous mor:* *F* layer well developed. Both *F* and *H* layers fibrous but not compact. Many plant remains visible also in *H* layer.

17. Effect of Humus on Forest Vegetation

Humus as a Source of Nutrients. — Humus is a source of supply of both ash and non-ash nutrients. The mineral constituents of leaves and other litter are returned to the soil and become available for absorption by roots after decomposition. The slow release of mineral nutrients in organic matter through decomposition gives results similar to rapid release through combustion by fire. However, mineral nutrients that are released at one time by combustion are often in part lost to the soil by runoff from the surface and leaching through the soil profile to the drainage waters.

In addition to the ash constituents essential for tree growth, others known as the non-ash constituents are always present in trees. They include carbon, oxygen, nitrogen, and hydrogen. Carbon is obtained by plants from carbon dioxide of the air and is used in photosynthesis. Hydrogen and oxygen are derived chiefly from water. These three elements are abundant in available form and need not be considered from the standpoint of soil fertility. However, nitrogen, which is absorbed by plant roots largely in the form of ammonia and nitrates, is

[1] Deep accumulations of organic matter of the mor type are sometimes called *raw humus*.

often limited in quantity. Ammonia and nitrates are formed through the decomposition of complex protein compounds by soil organisms. A large part of the total nitrogen in the soil remains in more or less stable organic compounds and in the protoplasm of organisms living in the soil.

The so-called mold fungi and both aerobic and anaerobic bacteria break down the cellulose in the litter (Waksman, 1932, 1936). Amino acids and ammonia are formed from the decomposition of organic matter containing nitrogen. The ammonia is oxidized by nitrite and nitrate bacteria to form nitrites and nitrates.

Hesselman (1926) has studied the problems of the regeneration of coniferous forests with particular reference to the formation of nitrates in the soil. He found nitrate formation and nitrate supply to be greatest under stands of beech and other deciduous species. They were usually poorest under coniferous stands where the ground is covered with moss.

18. Sources of Available Nitrogen in Forest Soils

Nitrogen in available form reaches the soil through:

1. Decay of organic matter, that is, through the formation and decomposition of humus.
2. Fixation of free atmospheric nitrogen by microorganisms, and their subsequent death and decay resulting in the release of available nitrogen.
3. Precipitation, which carries more or less combined nitrogen into the soil.

Soils lose their nitrogen by:

1. Removal of vegetation, that is, by not permitting it to die and decay in place.
2. Leaching, that is, through removal in the drainage waters.
3. Release of free nitrogen to the atmosphere during the process of denitrification.

19. Physical Effect of Organic Matter on Forest Soil

The effect of organic matter on the physical properties of soil is of great importance through (1) the action of incorporated humus particles which may be intimately mixed with the mineral soil, and (2) the effect of organic débris accumulated on the surface. The incorporated humus improves soil structure, increases water-holding capacity and percolation rate, decreases the volume weight, and is used by soil organisms as food. Humus causes light-textured soils to be more cohesive, and improves their structure and power of water absorption and retention. Heavy-textured soils, such as clays, are made more permeable to both air and water by the incorporation of humus. In addition,

humus has a high exchange capacity; being highly colloidal it has the power to adsorb and retain for future plant use many of the ions, such as calcium, magnesium, potassium, phosphates, and ammonia, which might be leached from the soil and lost in the drainage waters. The unincorporated organic matter protects the soil from excessive direct insolation, and from the compacting effect of heavy precipitation.

20. FOREST SOIL ACIDITY (REACTION)

Under climatic conditions where water percolates downward through the soil profile at least a part of the year, bases are leached from the soil; and, if the decomposition products of organic débris are highly acid, as is often the case under conifers, the exchange complex of soil may become highly unsaturated with bases, saturated with hydrogen ions, and the reaction of the soil solution will be highly acid. Soil reaction or acidity is expressed as the weight of free, dissociated hydrogen ions in a liter of water at 20° C. (68° F.). The H-ion concentration is usually written as pH, which is the reciprocal of the logarithm of the weight in grams of hydrogen ions in a liter of solution at 20° C. At pH 7 a solution is neutral; but alkaline solutions have a pH greater than 7 and acid solutions have a pH less than 7. Excessive acidity in forest soils may be harmful because of the effect on soil organisms which break down organic matter, releasing mineral nutrients, and making available nitrogen for higher plants.

Acidity of the soil may affect tree growth by checking the activity of nitrogen-fixing bacteria and of earthworms, by deflocculating clay, and by decreasing the solubility and, therefore, the availability of salts. On the other hand certain species, particularly of the family Ericaceae, grow best on acid soils. Wherry (1922), in studying soil acidity preferences of 23 conifers of the eastern United States, found that more than half of them grew on acid soils. Sundling, McIntyre, and Patrick (1932) found that the best seedling development of jack pine, red pine, white pine, and Norway spruce occurred between pH values of 4 and 6, except in the Hagerstown soil series, where pH values around 7 (neutrality) showed the best seedling growth. Scotch pine, according to Aaltonen (1925) and Schmidt (1930), germinates best at a pH of 5.4 to 6.0. Korstian (1924) found that southern white cedar grows and reproduces well in soil having a pH of 4.5 to 5.0; Wilde (1934, 1946) suggests that, for nearly all species, the most desirable reaction of nursery soil lies between pH 5.0 and 6.0. He concludes that a soil reaction less than pH 4.5 is unsatisfactory because of unfavorable influence of toxic soil compounds and low availability of nutrients and

that a reaction higher than pH 6.5 is very undesirable in seed beds, since it provides the optimum condition for the development of damping-off fungi, eel worms, and other soil organisms that cause the death of tree seedlings.

Forest vegetation may tolerate wide ranges in pH. Despite this toleration Cain (1931) concludes, from studies in the Great Smoky Mountains of North Carolina and Tennessee, that the higher acidities exert a considerable influence on the composition of forest communities. He attributes this partly to the direct influence of acidity and partly to the indirect influence of mor and peaty soils and accompanying factors on the elimination of species. Coile (1933) concludes that the soil reactions under seven different forest types in the Duke Forest in central North Carolina do not differ greatly enough to be a limiting factor in the distribution of forest communities. The kind of vegetation and the nature of the humus layers largely determine the degree of acidity in any particular environment. He reports that litter of low H-ion concentration appears to be decomposed more rapidly and the decomposition products incorporated more rapidly into the mineral soil than litter of relatively high H-ion concentration. Red gum, yellow poplar, red maple, river birch, sycamore, and dogwood are given as examples of litter of low H-ion concentration. Red cedar tends to make the surface soil more alkaline if the surface soil without a cover of this species is ordinarily acid.

21. SOIL CHARACTERISTICS AND HEIGHT GROWTH

Recently a number of efforts have been made to correlate site quality, as indicated by site index, with soil conditions. Hicock et al. (1931) related certain soil characteristics to the site index of red pine in Connecticut. They found a positive correlation between the moisture equivalent of the *A* horizon and site index, but only a slight correlation between colloidal content and site index. The total nitrogen content of the *A* horizon showed a better correlation with site index than any other factor studied by them. In general they observed fairly high correlations between low site indices and low values of the factors analyzed. Haig (1929) related site index in young red pine stands in Connecticut to the colloidal content of the *A, B,* and *C* horizons and to averages of combinations of these horizons, and to the silt and clay content of the *A* horizon. He found a definite positive correlation between site index and these values for the *A* horizon, which were better than similar values for the *B* and *C* horizons. Coile (1935), in a study of the relation of certain physical properties of soil to site

index for shortleaf pine in the Duke Forest, found no well-defined correlation between site index and any one physical characteristic or component of any one horizon. However, he found that " the quotient obtained by dividing the silt and clay content, or the colloidal content, in percent, of the B_1 horizon by the average depth in inches below the surface at which that horizon is encountered . . . [is] a reliable measure of site quality for shortleaf pine on the soils studied. The use of this texture-depth index should be of value in determining the site quality for shortleaf pine of soils having a relatively light-textured surface soil and a heavy subsoil located in regions where rainfall during the growing season is intermittent and prolonged dry seasons occur."

In later studies Coile[1] evaluated the relation between certain physical properties of the soil and the site index of loblolly and shortleaf pines in the lower Piedmont Plateau of North Carolina. Results indicate that the depth of the surface soil and properties of the subsoil that affect water movement and availability and aeration are most significant in determining site index for these pines. The results of this work make possible the estimation of site quality of land for pine forests regardless of the nature or age of the present cover.

22. EFFECT OF FIRE ON FOREST SOIL

Forest fires modify the nature and amount of nutrients in the soil, especially those derived from humus. Heyward and Barnette (1934) have shown that soils in the longleaf pine region subjected to frequent forest fires are less acid in reaction and contain a greater amount of total organic matter, nitrogen, and replaceable calcium. The observed changes in chemical composition of the soil ascribable to fire were restricted to the upper 4 to 6 inches. Replaceable calcium totaled as much as 101 percent more in burned-over soils than in corresponding unburned soils. The differences in total nitrogen were small but significant, ranging up to 14 percent more in soils subjected to fire. The authors attribute the changes in acidity and in replaceable calcium to the addition of ash following fire. They believe that the differences found in organic matter and nitrogen are due to differences in the forest floor and living ground cover as a result of burning. The unburned areas studied had a layer of pine leaf litter 2 to 3 inches deep and a scant living ground cover except in openings. On the other hand, the

[1] T. S. Coile, 1946. Relation of soil characteristics to the site index of loblolly pine and shortleaf pine in the lower Piedmont region of North Carolina. (Unpublished manuscript.)

frequently burned areas were characterized by only a small amount of litter but had a typical ground cover of wiregrass and a wide variety of broadleaved herbaceous plants, including numerous legumes.

23. MICROORGANISMS IN FOREST SOIL AND THEIR RELATION TO SOIL FERTILITY

The silvical importance of animals and plants that live in the soil has been increasingly stressed in recent years. Fertility of forest soils is to a large extent dependent on the organisms that reduce the organic remains of higher plants, mix them with the mineral soil, and further decompose humus rendering available essential plant nutrients.

24. Plant Life in the Soil

Forest soil is populated by a great variety of microorganisms (Bornebusch, 1930; Waksman, 1932). These organisms and their relative numbers are directly related to the growth and survival of forest vegetation. The essential conditions for their existence not only include the presence of air and water, suitable temperature, and the absence of toxic materials but also, primarily, an adequate supply of energy-producing food. The organic material in the soil is the source from which the energy is obtained.

The requirements of microorganisms for nutrients in soil are in the main the same as those of the forest vegetation itself. The chief distinction is that the soil population, with the exception of algae, depends on the organic matter in the soil for a food supply. Some of the organisms are useful to forest vegetation and some are harmful. Some act directly on the vegetation and others indirectly. Thus parasitic and disease-producing organisms, damping-off fungi, symbiotic organisms, bacteria living in nodules on the roots of leguminous plants, as well as mycorrhizae on the roots of trees, act directly on trees and other plants.

Fungi and bacteria are of even greater importance than animals in soil because of their rôle in decomposing organic matter and in producing nitrogen in available forms. Forest soils are especially rich in many species of *Basidiomycetes,* as evidenced by the numerous fruiting bodies which appear in summer. Numerous other fungi are present which do not reveal themselves above ground. Bacteria occur in all fertile soils. They are most abundant near the surface, where they often number 0.5 to 1 million per gram of soil. Nitrifying bacteria are of prime importance in producing available nitrogen for the growth of higher plants.

By far the most important class acts indirectly on forest vegetation. The organisms of this class bring about changes in forest soil which are indirectly of vast and far-reaching importance to the vegetation. Although they do not live in or in contact with the roots of trees, their relative abundance in a large measure determines the degree of availability of nutrients in the soil and as a consequence the growth and vigor of vegetation, as in *Azotobacter*, which changes the nitrogen from non-available to available form. They are essential to soil fertility.

The many species of algae which occur chiefly in the upper few inches of soil are capable of accumulating energy through the assimilation of carbon dioxide. There is also some evidence that they take part in the fixation of free nitrogen either directly or by symbiosis with certain bacteria (Frank, 1889).

The fungous flora of forest soil is largely confined to the upper 6 inches of soil. Unlike most other groups of the soil population, fungi appear to have the power to tolerate high acidity. They obtain their energy chiefly from the cellulose of organic matter and are important in its decomposition. Among the great variety of fungi that inhabit forest soils, those usually most abundant are various species of *Penicillium* and *Mucor*. Those most likely to have the greatest influence on forest vegetation, aside from hastening the decomposition of organic matter, are various species of *Fusarium*, *Aspergillus*, and *Cladosporium*, some of which are the chief causes of damping-off in young seedlings. It is now believed that fungi are, with few possible exceptions, without the power of fixing gaseous nitrogen (Duggar and Davis, 1916). Many of them, however, are important humus formers owing to their power to break down cellulose.

Infertile soils may contain toxic substances of biological origin which operate directly to inhibit the growth of fungi, which inhibition results in almost complete cessation of cellulose decomposition. Application of organic compost was found by Rayner and Neilson-Jones (1944) to remove the toxicity and profoundly to alter the organic substrate and the relationships of the soil organisms in an infertile heath soil in England. The resulting changes were found to be self-propagating and the beneficial effects on growth of forest-tree seedlings persistent. These beneficial effects were accompanied by rapid increase in mycorrhiza formation, pronounced growth of short roots, and increased absorption and supply of nutrients.

The bacterial flora of forest soils may be both harmful and beneficial. There is some evidence that certain forms produce substances in soil that are toxic to vegetation, and others assimilate nitrates, thus reduc-

ing the supply available for trees. In the main, however, soil bacteria are beneficial in that they are important in the decomposition of organic matter and in making available its nitrogenous constituents in the form of nitrates and ammonia. Both the rapidity of decomposition of organic matter and formation of available nitrogen are of such basic importance in determining the amount of available nutrients that a close relationship exists between bacterial activity in forest soil and rate of tree growth.

Conditions which cause excessive soil acidity bring about a reduction in the bacterial population of forest soil and consequently a reduction in ammonifying and nitrifying power. Alkali salts also affect soil bacteria adversely. Fluctuations in number of soil bacteria may also be inversely related to the number of active amoebae in a soil (Russell, 1932). A rise or fall in number of amoebae usually causes an inverse fluctuation in bacteria on which they feed.

The general level in number of organisms that constitute the soil population depends on the amount of energy available in humus colloids which coat the soil particles. Although the addition to soil of a single substance may favor the increase of a single group of organisms, the addition of complex organic substances from humus decay favors the increase of many groups of organisms. They provide energy not only for a larger soil population but also for a larger variety of organisms in the population.

Stoklasa (1927) and Fehér (1933) have recently emphasized the rôle of bacteria in soil respiration, more particularly in increasing carbon dioxide in the lower strata of air above forest soil. As the rate of photosynthesis, under a given light intensity, varies with amount of carbon dioxide in the air in contact with the leaves, this increase in carbon dioxide increases carbon assimilation and consequently increases growth in forest vegetation. Stoklasa also points out the further rôle of soil bacteria in rendering available, for trees and other forest vegetation, insoluble or partially insoluble mineral salts by chemically altering them into soluble compounds. There is, therefore, an increase in available nitrogen, phosphorus, and potassium in the soil due to the increased energy from the multiplication of microorganisms.

25. Mycorrhizae. — A most interesting explanation of the ability of trees to acquire nitrogen from raw humus has grown out of the discovery that tree roots are regularly invaded by symbiotic soil fungi (Frank, 1885). These invasions result in the formation of structures which are neither roots nor fungi but rather are compound organs in many respects comparable to the dual fungus-alga bodies of lichens.

Such an invaded root tip is termed a *mycorrhiza* (plural *mycorrhizae*).

26. Types of Mycorrhizae. — The roots of almost all plants are regularly invaded by mycorrhizal fungi (Kelley, 1932; Asai, 1934). Despite the diversity of fungi and of vascular plants concerned, nearly all mycorrhizae may be grouped into one of three types:

1. *Endotrophic,* in which the mycelium forms coils and various swellings within certain groups of cells of the primary root cortex.
2. *Ectotrophic,* in which the fungus forms a complete envelope over the exterior of the root (isolating it from the soil) and penetrates between, separating from one another, the cells of the primary root cortex.
3. *Ectendotrophic,* in which both of these types of infection are combined. It is convenient to lump the ectendotrophic with the ectotrophic mycorrhizae, since they seem to represent merely a stage in the development of ectotrophic mycorrhizae; and one mycelium, with rare exceptions, may give rise to both the intercellular and intracellular hyphae (Hatch and Doak, 1933).

Whether a tree species produces ectotrophic or endotrophic mycorrhizae is determined, at least in part, by the characters of the growing root tips. Those groups of trees whose roots are differentiated into two anatomically different types, (1) *long roots*, and (2) *short roots*, invariably produce ectotrophic mycorrhizae (only the short roots ordinarily becoming mycorrhizal). Trees with this type of root system include all members of the Abietineae, among conifers, and of the Salicaceae, Betulaceae, Fagaceae, and the genus *Hicoria* and a few other broadleaved trees. Those trees whose roots are all of one type or are merely segregated into *coarse roots* and *fine roots* possess endotrophic mycorrhizae. These include practically all other trees since there are very few species which wholly lack mycorrhizae.

27. Prevalence of Mycorrhizae in Trees. — Recently an extended field survey in northern Europe and in North America revealed that in natural forest environments about 95 percent of all tree roots are normally mycorrhizal (Hatch and Doak, 1933; Hatch, 1937). Although many observers have reported mycorrhizae to be similarly abundant in forest-grown trees, doubt has always existed as to the extent of the habit. The confusion is partly a result of examining tree roots growing in cultivated and garden soils, where mycorrhizae are often scarce or absent because of high availabilities of soil nutrients; partly because short roots are less conspicuous than long roots and only short roots normally become mycorrhizal (in trees with ectotrophic mycorrhizae); and partly because of erroneous assumptions. It was once believed that trees with endotrophic mycorrhizae lack infection because external appearances do not reveal the presence of the fungus. Again the

erroneous idea has prevailed that the presence of fruiting bodies of mycorrhizal fungi around trees serves as a measure of the numbers of mycorrhizae produced with their short roots. With the exception of one investigator (McDougall, 1927), all who have published more than one series of observations on tree roots in nature agree in finding them to be universally normal and widespread in forest environments (Hatch, 1937).

The identity of fungi producing mycorrhizae is well known only for trees having ectotrophic mycorrhizae. In these, various *Basidiomycetes* are involved, especially members of the *Boletaceae* and *Agaricaceae*, mushroom-fungi so common in forests during warm, wet weather (Melin, 1925; Doak, 1934; Hatch, 1937). Among trees with endotrophic mycorrhizae, the fungi have not been positively identified although there are many indications that they belong to the *Phycomycetes.*

28. Rôle of Mycorrhizae in Tree Nutrition. — This has been a moot question ever since Frank (1885) first suggested that they replace root hairs as normal absorbing organs. Many observers contend that the fungus performs no function useful to a tree after entering the root and that its attack is purely pathogenic, although only mildly so (Hartig, 1886; Sarauw, 1893).

In the more generally accepted organic nitrogen theory of ectotrophic mycorrhizae, it is proposed that the advantages of two distinct modes of life are pooled with mutual benefit (Melin, 1925). The fungus, capable of utilizing the complex organic nitrogen of raw humus, loses nitrogen to the tree while penetrating into the roots from which it, in turn, obtains carbohydrates — synthesized in the leaves. By means of this mutually beneficial, reciprocal parasitism (symbiosis), trees are presumably enabled to extend their ranges far into the arctics where raw humus soils, which are low in nitrates and ammonium salts and rich in organic nitrogen, would ordinarily exclude the possibility of tree growth (Melin, 1925, 1927).

Rather than being special symbiotic organs for overcoming nitrogen deficiencies alone, mycorrhizae are involved in the acquisition of at least three other elements, namely, phosphorus, potassium, and calcium. If, as is usual in forest soils, any of these four elements are available in less than optimum quantities, mycorrhizae become highly developed (Fig. 9), and the quantities of nitrogen, potassium, and phosphorus absorbed may be several hundred percent more than in non-mycorrhizal seedlings (Hatch, 1936; Mitchell et al., 1937). From both widespread nursery failures and experiments involving the use of

pure cultures of mycorrhizal fungi for inoculating prairie or infertile agricultural soils, trees are known to be incapable of existing in the absence of symbiosis with these fungi (Hatch, 1936; Young, 1936; Mitchell et al., 1937). By contrast in soils characterized by high and balanced nutrient availability, as sometimes occurs in fertilized and cultivated agricultural soils, mycorrhizae may be almost wholly absent. Here they could not be of much use because the unaided roots are quite capable of absorbing sufficient nutrients to maintain growth.

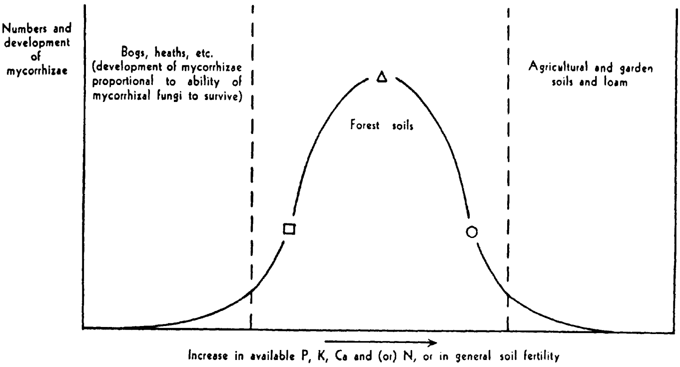


FIG. 9.—Schematic diagram illustrating relations between distribution, number, and development of ectotrophic tree mycorrhizae in nature and availability of nutrient elements (and general soil fertility). On the curve the square (□) represents an exceptionally infertile arctic raw humus soil of Sweden, the triangle (Δ) an infertile ridge soil in New York State, and the circle (○) a rather fertile cove soil in New York State. (*From Hatch, 1937.*)

Thus the known mineral salt theory of Stahl (1900), namely, that mycorrhizae are concerned with the absorption of all nutrient elements and that they are more efficient than roots in this process, is being revived. The basis of increased efficiency, at least in trees with ectotrophic mycorrhizae, is apparently the greatly increased surface areas of those short roots which are converted to mycorrhizae (Fig. 10).

An accurate knowledge of mycorrhizae may play an important rôle in future forest plantings. Mycorrhizal fungi are lacking in nonforested or denuded regions and must be introduced if trees are to survive (Hatch, 1936). Furthermore, the site requirements of these fungi are often more exacting than those of trees with which they are associated. Therefore, it is possible that the planting of trees possessing mycorrhizal fungi that are poorly adapted to many sites is one of the chief factors contributing to plantation failures. In the future it

may be advantageous to inoculate nursery stock with fungi that are adapted to the soils in which the trees are to be planted. Rayner (1934, 1936) working in Great Britain, found that where mycorrhizal development is deficient the condition can be improved and tree growth stimulated by inoculating seed beds with small amounts of suitable material containing active mycorrhizal fungi of the species. Under environmental conditions leading to soil drought, stimulus for renewed growth is provided in absorption of moisture by mycorrhizae (Cromer, 1935).

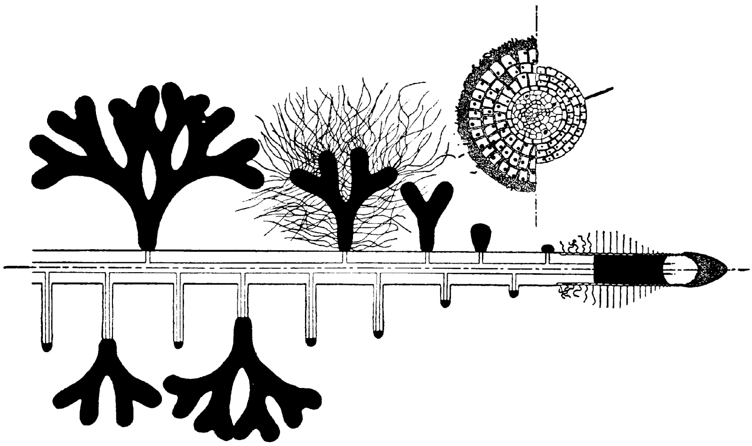


FIG. 10.—Schematic diagram of a long root of pine and of short roots. The short roots on the upper side of the long root represent short roots which were converted to mycorrhizae as they emerged from the long root. Of those on the lower side, only two show infection and at different intervals after emergence. Solid black represents absorbing surfaces. Non-mycorrhizal short roots have only insignificantly small absorbing surfaces. The cross-sectional halves of mycorrhizal and non-mycorrhizal short roots illustrate the character of fungus invasion and the changes induced by ectotrophic mycorrhizal fungi. (*From Hatch, 1937.*)

29. Animal Life in the Soil

The organic and upper mineral horizons of forest soils support a mixed population of soil animals which play an important rôle in the development of forest soil. They influence the soil in the following ways:

1. Increase porosity and aeration by their tunnels and passages.
2. Promote crumb structure and facilitate decay by mixing organic matter and mineral soil in their intestines.

3. Mechanically reduce organic matter.
4. Facilitate decay by burying organic matter.

Bornebusch (1930) working in Denmark found several animals characteristic of deciduous forest mull. Earthworms (50 to 80 percent of the weight) riddled topsoil and mixed it with organic matter from the soil surface. Millipeds were also common. He found that the slower the decomposition the lower the total weight of animals per square meter and the greater the number of arthropods. In spruce forest mor earthworms were scarce (rarely exceeding 10 percent of the weight) and the animal population, by weight, was made up largely of arthropods. Bornebusch states that "of the most striking significance in the forest are the larger earthworm species (*Lumbricus terrestris*, *L. rubellus*, and *Allolobophora turgida*) riddling the topsoil through and through and mixing it with deciduous organic matter. The deep and friable mull soil, as we find in deciduous forests, is contingent upon the activity of these animals." Many earthworms are found under clumps of dogwood trees on upland soils and in the red gum-yellow poplar forest type on the alluvial bottomland soils in the Duke Forest, the humus type in both instances being a mull.

Heyward and Barnette (1936) working in the longleaf pine region of the southeastern United States found evidence of intense animal activity in the A_1 horizon. They state that "this horizon, sometimes to a depth of 3 inches, is a labyrinth of small animal burrows. Many holes occur which lead vertically downward to undetermined depths, or downward for less than an inch where they connect with horizontal tunnels." They found that the A_1 horizon of soils heavier in texture than fine sand was definitely mull-like in character. Earthworm casts were abundant, and the soil was frequently of fairly good crumb structure to a depth of 2 inches.

Forest soils may contain both nematodes and protozoa among the microscopical inhabitants. The former are decidedly injurious, as some of them make their way into roots. The protozoa usually occur in large numbers in forest soils. They are normal inhabitants of all soils that are well supplied with organic matter but vary greatly in numbers from season to season and even from day to day.

30. SOIL STRUCTURE AND SOIL FERTILITY

The structure of soil may be as single particles or as compound particles. Compound particles involve the so-called crumb structure, a condition usually associated with high fertility. In practically all good soils, both forest and agricultural, the single-particle structure is

never predominant. The more important reasons for differences in structure lie in the differences exhibited in different soils in their base content, especially calcium, their temperature relations, and their biological factors.

Calcium and other bases flocculate the colloids in the soil, causing the particles to combine in small aggregates with more or less irregular spaces between. Usually the more lime in the soil the more granular its structure. Not all bases, however, are favorable to granular structure. An excess of a soda or potash salt by its electrical dissociation gives rise to an excess of OH ions which effectively prevent flocculation, as in alkali soils. In the burning of forests, the calcium and potassium from the ashes is harmful to basic soils but beneficial to acid soils from the standpoint of soil structure.

Freezing brings about the formation of ice crystals in the soil and causes more or less effectual separation of granules into compact aggregates between the crystals.

Among the biological factors which further the formation of compound particles in the soil, characteristic of the " crumb " condition, are earthworms. Insects and other animal life are also more or less effective (Bornebusch, 1930).

The crumb structure improves soil aeration, ease of root penetration, and water-holding capacity. It also increases pore volume and, in general, the greater the pore volume the better the soil. By rendering the soil less compact it greatly decreases volume weight of the soil. The extent to which the properties of separate particles are modified by being bound together in compound particles of various sizes and forms is unknown.

The desirable crumb condition of fine-textured forest soils can be destroyed by permitting the litter and the resulting humus to become greatly reduced by mismanagement or abuse. This is particularly true in soils where calcium carbonate is deficient. Under these conditions the soil loses its open texture, its clay properties are emphasized, and it becomes hard and compact on drying. It is likely to be sticky when wet, and air and water can penetrate between its particles only with extreme slowness. The development of the crumb condition in forest soils is a slow process. It is hastened by the presence of earthworms and myriapods and by an adequate supply of organic matter.

31. SOIL TEMPERATURE

Soil temperature in relation to the growth and development of forests has received but little attention. The studies of Halsted and Waksman

(1917) show that shoots of corn seedlings vary in development directly with temperature of the soil. Cannon (1916) in his studies on *Opuntia versicolor*, moved to a region of a cooler summer climate than its natural habitat, found that, when the soil was artificially heated, active root growth took place, and the plants put on new shoots and fresh leaves. Similar plants showed little or no new growth under the normal temperature conditions of air and soil.

The rapid increase in growth of tree seedlings after partial or complete removal of an overstory is probably due in no small part to the marked increase in temperature of the surface layers of soil. This is particularly true of trees growing in regions cooler than optimum for the species.

There are few available soil temperature data as compared with air temperature data, as very few U. S. Weather Bureau stations take soil temperature. The capacity of a soil to absorb, retain, and distribute heat determines in no small measure its quality for the production of a particular species. The functional activity of tree roots depends on temperature of the soil and increases with increase in soil temperature up to the optimum for the species. Cannon (1918) found that maximum root growth of *Larrea tridentata* does not occur until the soil reaches temperatures of about 90° F. A plant may wilt in a soil saturated with water sufficiently cold, because the plant can not absorb water. Kramer (1934) states that lowering the temperature of soil directly decreases absorption of water in two ways: (1) by its physical effects (chiefly increased viscosity and decreased vapor pressure), which result in a slower movement of water from soil to root and a decreased water-supplying capacity; and (2) by its physiological effects on permeability of root cells.

A plant may be killed by a soil temperature that is too low although it may safely withstand an air temperature many degrees lower (Warming, 1909). Shallow-rooted species, when growing in the open, have their roots subjected at times to much higher temperature than that of the air, owing to insolation. One of the most important effects of high soil temperature on forest vegetation is its effect on young seedlings which start in the open. The uppermost soil layer in the open may reach a maximum temperature 40 to 60° F. above the maximum air temperature 6 inches above the soil surface. Seedlings starting on bare soils are exposed at times to very high temperatures at, or near, the surface. As a consequence, lesions are formed on the stems, owing to excessive heat, and the young plants may be seriously injured or killed outright. This is an important reason for the better survival of

young seedlings under partial cover than in the open (Toumey and Neethling, 1924).

The heat of the soil depends upon duration of direct sunlight and angle of incidence of the sun's rays. In polar regions duration of sunlight plays a most important part. The nearer the sun strikes the soil at right angles the greater its heating power. Latitude, slope, and exposure all affect this result. The marked difference in vegetation of north and south slopes is largely due to differences in soil temperature (Bates, 1923, 1924; Pearson, 1931). Shreve (1924) has concluded that the difference between vegetation of north and south slopes is due to a group of conditions initiated by differences in insolation and soil temperature. The snow line is much lower on north slopes for the same reason. Soil temperature decreases with increase of altitude.

The specific heat of soils varies with its composition. Quartz sand heats quickly; peat heats very slowly. The amount of water in soils is of great significance in its influence on temperature, as water has a specific heat far greater than that of soil. Dry soils heat quickly but soils containing much water retain heat longer. Thus desert soils are very warm in the day and cold at night, because they rapidly lose their heat by radiation. Clay soils are cold because they retain large quantities of water.

The darker the soil, other things being equal, the more regularly and rapidly it is heated by the sun's rays, owing to its greater absorptive power. Dark soils cool more rapidly than light soils, owing to their greater loss of heat through radiation. A porous, gravelly soil absorbs the sun's heat very rapidly and becomes highly heated on the surface. The heat, however, is quickly lost. The conductivity of heat is greatest in rocky soil, particularly that containing limestone. Loose soil conducts heat slowly because of the larger air spaces. Vegetation that covers the soil affects soil temperature because it shields the soil from direct insolation and evaporation and intervenes in preventing loss of heat by radiation.

32. Shrinking and Swelling of Soil Under Action of Frost

Soils which contain an excess of clay or organic matter are subject to shrinking and swelling under the action of frost because of the large amount of water which they absorb. Young trees growing on them are frequently heaved by frost action during periods of alternate freezing and thawing in late winter and early spring. The consequent damage in nurseries and in newly made plantations is often very serious. The

danger can be overcome in nurseries by protecting young plants with a mulch of leaves during the winter or by otherwise shading them from the direct rays of the sun. Forest plantations should never be made in the autumn on soils where there is danger of the plants being heaved by frost. Haasis (1923) has studied the character and extent of frost heaving in ponderosa pine seedlings in northern Arizona. He shows that the greater part of the injury is in the first winter; 16.5 percent of all first-year seedlings observed showed effects of heaving and but 8.3 percent of older seedlings.

33. Fluctuations in Soil Temperature

The mean daily temperature of exposed soil is higher in winter than that of the air. The temperature of exposed soil during the day in summer is considerably higher and during the night usually slightly lower than that of air. The daily range is greatest at the soil surface and gradually decreases with depth until it vanishes altogether. Compact soils that are good conductors of heat show daily fluctuations at greater depths than loose soils. The daily range at the depth of 1 foot seldom exceeds 5° F. at any period of the growing season, and at 2 feet it is seldom more than 1° F. Moore (1911) states that at 45° latitude the diurnal changes are not appreciable below a depth of 3 feet. Forest soils protected by an overstory or otherwise shaded have a much lower daily range, particularly at the surface. Seasonal fluctuations in soil temperature penetrate to much greater depths than daily fluctuations. A difference between winter and summer temperature is often discernible at a depth of 20 or more feet.

34. Influence of Soil Temperature on Form of Forest Vegetation

The effect of soil temperature on the form assumed by trees and other plants is uncertain. High soil temperature according to Vesque (1878) gives rise to an abundance of sap and to short and thick roots, stems, and leaves. Low soil temperature, on the other hand, causes a diminution in amount of water and nutrients absorbed. This causes dwarfing, so characteristic of trees growing in cold soils. Willows and some other woody plants often assume prostrate forms in such soils. A naturally warm soil is favorable to early germination of seed, early start of vegetation, rapid decomposition of humus and, as a consequence, a larger production of timber. A cold soil tends to an excessive accumulation of organic matter. Growth, checked, starts later in the spring. Warm soils are more variable in temperature than cold soils owing to their greater loss of heat through radiation on cold nights. Vegetation

growing in warm soils is more subject to injury from spring frosts. Cannon (1917) in a study of root growth in seedlings of mesquite in southern Arizona found that the temperature at which root growth in this species took place ranged from about 53.6° F. as a minimum to about 107.6° F. as a maximum, but that the optimum growth for individual seedlings was at a variable temperature between these two extremes.

35. Soil Temperature in Forests as Compared with the Open

It has long been known that soil temperature, particularly during the growing season, is influenced markedly by mature, fully stocked forests. This is especially true of the surface soil layers, where fluctuations from hour to hour are the greatest. As the chemical and biological processes which promote root growth are largely dependent on soil temperature, it plays a very important rôle in natural regeneration, and in determining the species that survive. The lowering of soil temperature under closed, natural forest canopies affects:

1. Length of time that seeds remain viable in the litter.
2. Germination.
3. Survival of young seedlings.
4. Development of seedlings.

One of the most important requisites for seed storage in the forest floor without deterioration is low temperature (Hofmann, 1917). Under natural conditions, seeds in the litter remain viable longer under a high forest of full density, owing to its effect in lowering surface temperature. Germination fails even when moisture and aeration conditions are at their optimum, if the temperature is too low (Hawley, 1922). Thus under a closed canopy of white pine in northern New England the temperature of the surface soil is too low for spring germination. This delay in germination seriously affects later survival. A heavy thinning increases the temperature of the surface soil and hastens germination.

Young seedlings, immediately after their emergence above the ground, are very susceptible to injury from high soil temperature. Surface soil temperature above 130° F. often proves fatal to young seedlings. Yet in nature a temperature of 152° F. has been observed at the surface of a denuded, sandy soil near Keene, New Hampshire (Toumey and Neethling, 1924). Comparably high and even lower temperatures of surface soil in the open have been reported by Hartley (1918), Korstian and Fetherolf (1921), and Bates and Roeser (1924), with accompanying injury to stems of coniferous seedlings, known as stem girdle, caused by excessive heat.

Under certain conditions maximum temperatures of the surface soil may prevent natural reproduction. It is clear that lowering of the surface temperature of the soil by a natural shade that is not too dense may be most important in bringing in a successful crop of young seedlings. Although deficiencies in light and soil moisture are important factors in accounting for poor development of most seedlings under dense canopies, Bühler (1918, 1927) states that soil temperature plays an important rôle. According to Huffel (1904) the flora and fauna under a forest are largely controlled by soil temperature, which in turn is determined by different species constituting the forest, and by different treatment. His view is substantiated by that of Cannon (1916).

The work of Pearson (1914) and Li (1926), reviewed more fully in Chapter XI, emphasizes the extent to which soil temperatures are modified by a forest cover as compared with soil temperatures of open land.

36. SOIL ATMOSPHERE

From a comprehensive review of the subject, Clements (1921) concludes that the air content of soil is of basic importance in plant ecology, although most plant physiologists and ecologists have ignored it until just recently. Notable exceptions have been the work of Cannon (1922, 1923, 1924, 1925) and Cannon and Free (1917, 1925), who conclude that many of the 30 species studied appear able to maintain root growth for a limited time in a soil atmosphere containing as little as 0.5 percent oxygen, provided the amount of carbon dioxide present is not as great as 25 to 50 percent. When oxygen is entirely removed from the soil air, no root growth occurs in any species. Vigorous seedlings are most resistant to deficiency of oxygen. In wet soils with consequent poor aeration and with high soil temperatures as in summer, the oxygen supply available to roots may be inadequate.

The supply of oxygen available in the soil is important in the germination of seeds. Although some seeds germinate well with exceedingly slow oxygen supply, others require a very rapid supply. Hutchins (1926) found that good germination of wheat occurs when well supplied with water and with temperatures about 72° F. in a soil with an oxygen-supplying rate of 3.0 mg. or more per square meter per hour; but rice seed germinates well when the corresponding value is as low as, or lower than, 0.5 mg. He reports that wheat failed to germinate at all with oxygen-supplying rates below 1.5 mg., but that rice germinated with the lowest rate tested in his experiments (0.08 mg.). Each kind of seed appears to have its own minimum oxygen requirement.

Air in the soil is also of fundamental importance for tree life. All parts of the tree below ground, like all living parts above ground. require oxygen for respiration. Trees, the life processes of which are adjusted for soils rich in air, are suffocated in very wet soils. When air with its contained oxygen is excluded, fermentation occurs in the roots with the evolution of CO_2, and as a consequence death and putrefaction follow. Diminished growth and final death of trees through lack of soil aeration are of common occurrence. Two distinct processes are involved:

1. Cutting off of oxygen needed for respiration in tree roots.
2. Accumulation of carbon dioxide in a non-aerated soil.

Cannon and Free (1917) have shown that certain species of trees respond differently to variations in composition of soil atmosphere. Roots of mesquite cease to grow in an atmosphere without oxygen or where there has been a replacement of normal atmosphere with carbon dioxide, but roots of willow continue to grow when almost completely deprived of oxygen. Willow appears to be quite independent of oxygen content in the soil atmosphere.

The aeration of soil depends primarily upon its structure; the more porous and loose the soil the better its aeration. The interstices between the particles of soil that are not filled with water are filled with air. The amount of air in any soil therefore depends upon the degree of wetness. Alluvial soils and loose mulch have the greatest capacity for air, often containing as much as 60 percent of the total volume. On the other hand, coarse gravelly sand may contain less than 10 percent, even where there is no free water present. Wet soils or those loaded with free water may have the air content reduced to much less than 1 percent of the total volume, the air being driven out by the water. In well-aerated soils, tree roots penetrate much deeper than in poorly aerated soils. They die back through asphyxiation when they reach a horizon in which there is a deficiency of air. It is chiefly for this reason that swamp trees are shallow-rooted and trees growing on well aerated soils are deep-rooted. Not only are deficient oxygen and excessive carbon dioxide in the soil determining factors in survival, but the degree to which soil is aerated is a factor in growth.

37. Adjustments to Poorly Aerated Soils

Owing to special adjustments, certain species of trees are able to thrive on poorly aerated soils. Sometimes the internal structure of a plant appears to be correlated with the amount of air in the soil. In

very wet soils, with few exceptions, only such plants appear to thrive as have large internal air spaces which communicate with each other and convey air from the shoot to below the water level.

Although the erect root branches of southern cypress and mangrove and the long surface roots of many swamp trees, such as swamp black gum, are undoubtedly reactions to swamp conditions, they are difficult to explain adequately as due to lack of air in the soil. The so-called plank roots, common in tropical species, are possibly due to lack of air in the soil. Greatly enlarged bases to the boles, as in tupelo gum, and southern cypress, are frequent in species growing in swamps. Although these swollen bases are of undoubted value in giving greater stability, they are believed by some to be a response to water plus air, and cypress knees, like buttresses, are believed to be reactions to water plus air exposure (Kurz and Demaree, 1934).

In cases of inundation all soils are deficient in oxygen, the only air remaining in the soil being that contained in water. Under prolonged inundation, therefore, species not provided with special adjustments suffer severely or are killed outright. Under ordinary conditions all forest soils, except those under water for more or less extended periods and those on which certain types of mor are present, contain air sufficient for most forms of forest vegetation.

In forestry practice special attention must be given to selection of species for use on heavy clays, in swamps, and on bottomlands subject to inundation. Shallow-rooted species should be selected for such sites. Swamp species, as illustrated in southern cypress, southern white cedar, willow, black ash, elm, and swamp black gum, will usually thrive on uplands when planted where the soil is capable of retaining moisture in the surface layers. On the other hand, upland trees seldom persist when transferred to soils that remain saturated with moisture for long periods.

38. Effect of Filling in Around Trees on Aeration

Trees are very often severely injured or killed by the filling in of soil around them, or by covering the soil with cement, macadam, or other material which cuts off air from above. The latter is one of the common causes of the death of trees in cities. Death in both cases results from asphyxiation. In filling in soil about trees the damage can not be wholly overcome by the common practice of building wells about the boles, as these wells have but little effect upon aeration. The character of soil used in filling in is of great importance. Fine

soils such as heavy clay should not be used. The use of coarse sand and gravel with an abundance of rubbish strewn over the surface before the soil is filled in results in least damage.

39. Toxic Soil Gases

In ordinary well-aerated forest soils, gases are seldom present which are harmful to vegetation or which influence its form or structure. In cities and towns, particularly along avenues and streets where gas mains are placed only a few feet below the surface, gas sometimes escapes and accumulates in the soil surrounding the roots of trees. The ethylene (C_2H_4) that it contains is toxic to the roots and when sufficiently abundant causes death of trees.

Deuber (1936) found that, when relatively large volumes (32 to 864 cubic feet) of a coke oven type of illuminating gas were flowed into soil in which young elm trees were growing, chlorosis and defoliation were the chief early symptoms, followed, sometimes, by drying out and death of terminal parts of branches and stems and the death of 2 out of 20 trees. He attributes the lethal and injurious effects of relatively large amounts and the stimulative effects of small amounts (5 to 10 cubic feet) of the gas to ethylene or other constituents having a similar physiological action.

40. EFFECT OF SILVICULTURAL PRACTICE ON SOIL CHARACTERISTICS

The development of thick accumulations of organic débris under coniferous forests in the northern part of the United States can be considered normal for that climatic régime. Under such conditions podsol soils develop, often with a pronounced hardpan. The development of the pan may cause a deterioration of the site. The decomposition of the heavy accumulations of organic matter on the soil surface can be hastened by opening the stands through thinning and by favoring the development of certain species — often hardwoods — whose mature litter contains a greater amount of bases. The less favorable mor humus types are often characteristic of northern coniferous forests. The development of a heavy mor humus type may make the reproduction of desirable species difficult or impossible unless steps are taken to reduce the accumulation of organic débris. This reduction may be accomplished by clear cutting, heavy partial cutting, burning, or by breaking up the humus cover while skidding logs or by plowing.

There is a tendency toward the accumulation of rather large amounts

of poorly decomposed organic débris on the forest floor under pure stands of conifers in the region of brown forest soils. This may be true particularly when the soil and parent material is low in bases, as in soils developed from acidic igneous rocks. Although the brown forest soils are podsolic they do not normally have the typical gray podsol *A* horizon. The presence of pure stands of coniferous trees under certain climatic conditions will result in the development of a true podsol with an *A* horizon low in bases and the sesquioxides of iron and aluminum, and often a hardpan in the *B* horizon. Such a condition represents soil deterioration, and it can be avoided or modified to a certain extent by bringing into the stand hardwoods whose litter has a higher nitrogen content or a higher base content. Fisher (1928) and Griffith, Hartwell, and Shaw (1930) observed changes in the humus type and upper mineral soil when pure white pine stands were replaced by mixed hardwoods in the Harvard Forest.

In general, there is not a deep accumulation of organic débris under deciduous forests in the brown forest soil region and farther south. Higher summer temperatures, longer summers, and adequate moisture promote more rapid and complete decomposition of litter as compared to the region of podsol soils. However, mor humus types are found even in the Southeast under pure stands of pine, and under oak forest.

The researches of Schütze (1871) throw some light on the relative importance of the chemical and physical properties of soil in forestry. He examined the soil of 6 site classes on which Scotch pine was growing under a rotation of 100 years. He found no direct relation between amounts of chemical soil constituents present and site classes, although, in general, soils of the poorer site classes contained slightly smaller amounts of phosphoric acid, calcium, magnesium, potassium, and sodium than the better sites. Many of the forest soils containing relatively small amounts of the essential mineral elements were among the best sites for the growth of pine. He found that there was a progressive increase in amount of fine soil particles from the poorest to the best sites, and he concluded that physical character of the soil, especially water-retaining capacity, was of particular importance in determining site quality.

The amounts of essential mineral constituents in the soil and the amounts used by forest vegetation are such that even soils low in them contain an excess (Schütze, 1871). Apparently the exhaustion of essential mineral constituents by forest cropping seldom takes place. A good site for Scotch pine would not be exhausted of the potassium required for plant nutrition in 10 successive crops and of the phosphoric

acid in 25 successive crops, even though there were no yearly replacements through the decay of litter and through weathering.

Although the exhaustion of essential mineral constituents of soil by forest cropping seldom occurs, it should be emphasized that under certain conditions chemical composition of the soil determines the availability of the minerals. Under certain conditions an excess of calcium and manganese salts may cause the iron to become combined in a colloidal form unavailable for plants. As a direct result the vegetation suffers from chlorosis or iron deficiency (Korstian, Hartley, Watts, and Hahn, 1921).

Forest and agricultural soils are vastly different in that agricultural soil, through tillage, loses its more or less distinct surface horizons. The soil to the depth of plowing is more or less homogeneous.

Under natural conditions, as trees die and disappear from the stand they are replaced by others. Regeneration is abundant. The more the method of reproduction departs from the natural, however, the greater the departure from normal forest soil and the greater the need for artificial treatment to obtain regeneration and to maintain soil fertility.

Normal forest soil, with its more or less well-defined horizons, is the result of the forest vegetation itself. There is no such thing as a normal forest soil on areas not stocked with timber or, in other words, on areas where trees do not grow in closed stands. The litter which is the first requirement for a normal forest soil is unattainable without a reasonably close canopy and competition among the trees. The development of normal forest soil with its successive layers from the litter downward requires a long period of years, but once developed it endures indefinitely so long as the forest cover is not destroyed or the canopy too extensively broken. Organic matter in forests serves the same function as tillage in agriculture in keeping the soil loose and in good physical condition. Remove the organic matter and forest soil becomes more or less hard and compact and growth decreases. Organic matter conserves moisture in the upper layers of soil within reach of the roots of vegetation.

Agriculturists maintain soil fertility through crop rotation and the application of fertilizers; foresters, by the maintenance of desirable humus conditions. Foresters are chiefly concerned with the litter and the resulting humus. Farmers have no litter to deal with in the sense that foresters have. A farmer is concerned in supplying nutrients and in seeing that through tillage they are intimately mixed with the top soil. He maintains and increases soil fertility largely by artificial

means; a forester through the medium of his crop of trees. A forester's task is the more difficult one, owing to the more complex character of forest soil and its constantly changing conditions, dependent on natural variations in density of the canopy at different times in the life of a stand. Furthermore, an agriculturist can often quickly build up depleted soil to its former fertility when necessity arises. Foresters, because of economic restrictions inhibiting the application of fertilizers, can not bring back misused and depleted forest soil to its former fertility except by long and laborious processes.

Although years are required to develop a normal forest soil, it may be destroyed by overexposure for a prolonged period, by repeated surface fires, by overgrazing, or by removal of the litter. It is as much the task of foresters to develop and maintain a normal forest soil as it is to obtain regeneration and make necessary cleanings and thinnings.

CHAPTER VII

SOIL MOISTURE AND ITS INFLUENCE ON FOREST VEGETATION

1. BASIC CONCEPTS

Forest vegetation obtains water needed for transpiration and growth entirely or almost entirely by absorption through roots imbedded in the soil.

The amount of water that reaches the soil is determined directly or indirectly by the amount of precipitation. The amount of precipitation varies greatly from one climatic region to another, and within a region it may show great seasonal and yearly variation. Soils located on the lower part of slopes or in depressions may receive a large part of their water as runoff from higher areas. In addition, subsurface water is an important source of supply to soils in certain topographic positions. The presence of a relatively impervious layer in the substratum will often bring ground water near the surface at the bottom of slopes. Also, the presence of an impervious stratum near the surface often results in a suspended water table all or a part of the year, making the site far more moist than its topographic position and soil properties would ordinarily indicate.

Water exists in the soil both as liquid and as vapor. The various forms of water in the soil can be classified according to forces involved in its movement or retention as follows:

1. Gravitational water
2. Capillary water
   - *a.* Interstitial
   - *b.* Adsorbed
3. Water of hydration

Gravitational water is that which is free to move under the force of gravity. Immediately after rains it occupies the soil air-space, but is soon removed to the ground water through action of the force of gravity. Gravitational water is of little use to plants because it remains in the soil only a short time. A few hours after a heavy rain a great part of it has moved deep into the soil.

The capillary elements of the soil can not be looked upon in mass as a large number of capillary tubes of different sizes. As Keen (1928)

has indicated, the pore space in soil may be regarded as consisting of an assemblage of small cellular or irregular, thread-like capillary tubes, irregular in width, length, and direction. The water held by film forces in the interstitial spaces between soil particles is used by plants. Its movement is extremely slow and uninfluenced by gravity, being determined by the size of interstitial openings, the viscosity of water, and the combined forces of adhesion and cohesion which cause water to wet the surfaces of soil particles and still maintain a continuous film.

In addition to interstitial capillary water, a small amount surrounds the particles which does not move as a liquid but as vapor. The interstitial water moves over the inner film of adsorbed or hygroscopic water. Parker (1922) found that free water, or interstitial capillary water, could be frozen the first time it was cooled to —1.5° C. (29.3° F.), but the adsorbed capillary water was frozen only at lower temperatures.

Water of hydration is in chemical combination with the secondary soil minerals that make up the clay and colloidal fractions of soils. It is unavailable to plants. Water of hydration and water combined with organic and inorganic colloidal gels is driven off when a soil is ignited.

2. MOVEMENT OF SOIL MOISTURE

Water moves in the soil both as vapor and as liquid. As vapor it moves from regions of high vapor pressure to regions of lower vapor pressure. Movement of water in the vapor state is of importance in soils whose moisture content is below the wilting percentage. It will move into a soil as vapor until a film of water surrounds each soil particle and the soil atmosphere is saturated with water vapor; from that point on water may move as liquid into the soil over the film which remains stationary at soil moisture contents greater than maximum hygroscopicity.

Lebedeff (1928) found that if soil contains moisture in excess of maximum hygroscopicity, then the relative humidity of soil air equals 100. He also observed that as the moisture content of soil decreased below maximum hygroscopicity the relative humidity of soil air as measured with a hair hygrograph decreased also. With the moisture content of soil constant the relative humidity of soil air increased or decreased with temperature changes. Veihmeyer and Hendrickson (1934) observed that water vapor absorption was materially influenced by the original moisture content of soil. Linford (1926) found that soils would absorb water in excess of the moisture content at the wilting coefficient when exposed to a saturated atmosphere in a dark, constant-

temperature chamber. He found that there is an equilibrium between a saturated vapor and a saturated soil, but did not find that there could be an equilibrium between relatively dry soil and saturated vapor as some workers have reported. Temperature affects movement of water vapor. Bodman and Edlefsen (1934) observed that diffusion of water vapor in soil is very slow and is greatly increased if there is a temperature gradient. By far the greater amount of vapor movement in soils is through the convection currents of soil air. Lebedeff (1928) considered the condensation of water vapor in the upper soil to be of considerable importance in the southern steppes of Russia. Evidence at the present time indicates that the movement of water in soil as a vapor is of greater importance than has been considered in the past.

The movement of water in soil as liquid is influenced greatly by the size of particles, and the size, shape, and continuity of the interstitial spaces. Water will move most rapidly in a sand and least rapidly in a clay. If a soil is completely saturated with water and then allowed to drain, water which moves out of the soil under the influence of gravity is of little use to vegetation; in fact, it may be harmful in that it may occupy air space necessary for good soil aeration. The amount of gravitational water that will move from a saturated soil is greatest in sands and least in clays.

The movement of soil water is caused mainly by gravity, hydrostatic pressure, and capillary forces, the last resulting from differences in the curvature and thickness of water films. Since it is often difficult to distinguish between these forces it is helpful to think of the movement of water along a gradient of decreasing free energy, and to remember that the work required to move water against the attractive forces of the soil increases as the soil moisture decreases. This work is often measured in terms of the height of an equivalent column of water or mercury and is designated as the " capillary potential " or " pressure potential " (Kramer, 1944).

At soil moisture contents below field capacity, water as liquid moves by film forces and is uninfluenced by the force of gravity. Magnitude of the film forces increases with decreases in the size of soil particles and interstitial openings. Water will rise a greater distance by capillary action in a clay soil than in a soil of coarser textural grade, but the rate of rise is slower.

The magnitude and importance of the movement of water by capillary forces have probably been overemphasized in the past. Shaw and Smith (1927) found no movement of water into soil from a water table 10 feet from the surface. Water was evaporated from the surface

of a sandy loam soil, but none was removed from the ground waters. Veihmeyer (1927) in studying the growth of trees in containers under controlled moisture conditions found that the application of water to the surface only affects the moisture content of the soil mass down to the depth to which it can be raised to maximum field capacity. Further movement is extremely slow and is offset by the removal of water by plant roots in the region of higher moisture content. Keen (1928) found that the upward movement of water by capillarity as a result of evaporation from the surface lowered the water table slowly after it had fallen to about 3 feet. He concluded that the supply of water by capillarity either to the soil surface or to the region of the actively absorbing roots is limited.

Therefore, it is likely that relatively little soil moisture moves toward the tree roots and that most soil water becomes available only as the roots come in contact with it as a result of their elongation through the soil.

3. SOIL MOISTURE CONSTANTS

The following soil moisture constants are often used in studying the interactions between soil and vegetation:

1. Hygroscopic coefficient.
2. Wilting percentage.
3. Moisture equivalent.
4. Wilting coefficient.
5. Field capacity.
6. Water-supplying capacity.

The *hygroscopic coefficient* is the amount of water that a soil will absorb when in equilibrium with a closed atmosphere saturated with water vapor. The value is difficult to determine because it is influenced by the original moisture content and chemical composition of the soil used and by light and temperature. Robinson (1932) states that a soil which contains no more moisture than is indicated by its maximum hygroscopic capacity is incapable of yielding water to plants or of permitting microbiological activity.

The *wilting percentage* is the amount of water remaining in a soil when plants growing in it have wilted permanently, that is, so much that they will not recover when placed in an atmosphere saturated with water vapor. This is perhaps the most useful soil moisture constant, since it determines the lower limit of water available to plants. The magnitude of the wilting percentage is largely a function of the amount of the finer fractions, clay and colloidal, in a soil. In general, organic

colloidal material will hold water more tenaciously than inorganic colloidal material.

The *moisture equivalent* is the amount of water retained by a soil that has been previously saturated with water after it has been subjected to a force of 1,000 times gravity for 30 minutes (Briggs and Shantz, 1912). It is a constant for a given soil and aids materially in characterizing texture and structure with only one figure. The moisture equivalent increases with the amount of clay and organic matter in a soil.

The *wilting coefficient* is determined by dividing the moisture equivalent by 1.84 (Briggs and Shantz, 1912). The use of the wilting coefficient as a means for determining the amount of available water in the soil is limited because the actual conversion factor necessary to approximate the wilting percentage has been found to vary greatly. Veihmeyer and Hendrickson (1934) compared the wilting percentages of more than 100 soils with their moisture equivalents. The ratios of the moisture equivalents to the permanent wilting percentages ranged from 1.39 to 3.82. Although the Briggs and Shantz ratio of 1.84 held for some soils, the departures from this value were considered too great and numerous to warrant its general use.

The *field capacity* is the amount of water left in a soil after the gravitational water has moved out. In many soils it is close to the moisture equivalent (Veihmeyer and Hendrickson, 1934). Field capacity percentages are most valuable if made on soils the natural structure of which is undisturbed (Coile, 1936). The field capacity of soils is influenced by texture, organic matter content, and structure. Kopecky (1928) stated that "quantities of rainfall being equal, the volume of water contained in soil at the disposal of plants varies largely, and is proportionate to absorbent power or water capacity."

The amount of water that a soil can supply to a porous surface has been used by Livingston and Koketsu (1920) to determine moisture conditions in a soil when plants wilt. Using soil-point cones, they found the *water-supplying power* of the soil to be 0.085 g. in 2 hours at the time of permanent wilting.

At low moisture contents water is held with much greater force than at high moisture contents, and there is only a slight change in the force from field capacity to about the permanent wilting percentage. Studies on the availability of soil moisture show that plants can use water with equal facility throughout the range of moisture contents from field capacity to about the permanent wilting percentage (Veihmeyer and Hendrickson, 1934).

4. WATER PERCOLATION IN SOIL

The rate and amount of water that will percolate into soil are dependent upon a number of soil characteristics and character of vegetation. They are influenced by the following factors:

1. Soil structure.
2. Soil texture.
3. Animal tunnels.
4. Cavities left by decayed roots.
5. Character of surface vegetation.
6. Compactness of soil surface.

Slater and Byers (1931) concluded that field percolation rate of soil is governed more by the water passageways, root channels, or structural cleavages it contains, than by character or volume of the soil mass. Auten (1933) found that the difference in field percolation rates of forest and field soils was related to the better structure found in forest soils. He found forest soils to be more porous and to absorb water much more rapidly than field soils. The soil under plantations on cultivated fields regained its porosity in 20 to 25 years after planting. Coile (1935) found a correlation between field percolation rate of Piedmont forest soils and site index of shortleaf pine; for site indices between 26 and 68, water absorption increased from 30 to 160 ml. per minute. He observed that waterways formed by soil animal activity and decayed roots are more important in determining rate of water percolation than cleavage planes and pore space.

The vast number of animal burrows found in long-unburned longleaf pine soils, as reported by Heyward and Barnette (1936), evidently play an important part as water passageways, particularly during torrential rains characteristic of that region. Livestock, when present in great numbers, cause compacting of surface soil and decrease its permeability to water. Forest fires, by removing the forest floor and discouraging animal activity, expose the soil surface to beating rain and excessive insolation which result in compaction, loss of crumb structure, and decreased permeability to water. Suspended particles in runoff water from bare soils are filtered out in the surface soil, sealing the pores and other seepage openings; but soils covered with forest litter maintain maximum percolating capacity (Lowdermilk, 1930).

5. LOSS OF WATER FROM SOIL

Water is removed from soil by transpiration of plants, by percolation to the drainage waters and subsequent removal, and by evaporation.

Although foresters can not control soil moisture fluctuations due to seasonal droughts, they can to a certain degree conserve soil moisture by forest management. Through proper management desirable litter and forest-canopy conditions can be maintained. An excessive thinning or a clear cutting on an exposed site may be followed by the disappearance of litter and the deterioration of soil. The complete uncovering of advance reproduction may result in its death. These are considerations which sometimes definitely determine what method should be used in handling a stand or even an entire forest.

6. Water Loss Through Evaporation

A large amount of water is lost from soil through evaporation. Climates which induce an excessive loss of soil water by evaporation support vegetation different from that on soils where the loss is less.

The conditions which determine intensity of evaporation from soil are both *external and internal*. The chief external conditions are:

1. Relative humidity of the atmosphere.
2. Velocity of the wind.
3. Slope and exposure of the surface.
4. Dead and living cover on the surface.

The greater the relative humidity of the air the lower the loss of water from the surface soil through evaporation. A slope or exposure where the surface is fully exposed to the direct rays of the sun loses water by evaporation more rapidly from its surface layers than from less exposed surfaces. Loss through evaporation is directly influenced by wind velocity; other things being equal the loss through evaporation is least when wind movement is lowest. The dead and living surface cover protects the soil from sun and wind and greatly reduces loss through evaporation. The living cover, however, may draw more water from the soil at times during the growing season to supply transpirational loss, than it conserves by shade.

The chief internal conditions are:

1. Moisture content of soil.
2. Compactness of surface soil.
3. Structure of surface soil.
4. Color of soil.
5. Size of soil particles.

Water evaporates more rapidly from compact than from loose soils and from dark than from light-colored soils. Soils with medium-sized particles permit greatest evaporation. The formation of crumb struc-

ture reduces evaporation. Evaporation from a soil saturated with water is greater than from a free water surface.

7. Water Loss Through Transpiration

The actual surface of vegetation in a forest exposed to the air is many times that of the soil. Furthermore, vegetation uninterruptedly extracts water from the soil through its roots. A little of this water is incorporated into the vegetation itself; the greater part, however, passes out of the leaves and other parts above ground through transpiration and is evaporated from the plant surfaces. An area covered with trees and other forest vegetation will lose more moisture from soil during the growing season than an absolutely barren area having similar soil conditions. The water loss through evaporation from the latter area is usually less than the loss from the former through transpiration and evaporation combined. The amount of water taken from the soil by roots of plants during the growing season depends not only on atmospheric conditions but also upon the kind of vegetation and soil temperature as well as upon the water present in the soil and its relative purity. Largely owing to the consumption of water by trees during the growing season, forest soil as a whole becomes progressively drier from spring to autumn.

The work of Höhnel (1884) shows a large loss of water from forest soil during the growing season owing to transpiration. The loss from a fully stocked, mature stand of spruce was more than 200,000 gallons per acre. Weaver and Crist (1924) give the transpirational loss from the tall grass prairie association in Kansas as approximately 1 pound of water daily per square foot of land surface throughout the growing season.

Forest vegetation tends to conserve soil moisture, through the living and dead ground cover, which, retaining precipitation that would otherwise be carried away in the surface runoff and through the ground cover, acts as a mulch in checking evaporation loss from the mineral soil beneath. On the other hand, forest vegetation tends to decrease soil moisture by interception of a part of the precipitation by the canopy and by the loss from the soil through transpiration. The surface soil under a forest may remain dry during light showers while that in the open is comparatively wet. Much water is held on the leaves and on the surface and in the crevices of the bark of stems and branches of trees until it evaporates into the air without reaching the soil (Horton, 1919; Phillips, 1926; Beall, 1934). The amount of water

thus lost to the soil may vary from 75 to 100 percent in light showers to about 25 percent in heavy rains of long duration.

The total effect of forest vegetation on soil moisture is the resultant of all factors which tend to increase and to decrease soil moisture. Simpson (1927) has compared the seasonal variations in soil moisture in a forest and in a similar site without vegetation. His studies show that the average moisture content of soils covered with stands of timber is much less over the growing season, down to a depth of 3 feet, than of similar soils denuded of all vegetation.

There was, in the region studied, a progressive depletion in soil moisture in the forest from early in the growing season (June) until after the growing season was over (October). On the other hand, soil moisture on the denuded site, after the marked reduction in spring, actually increased from June to October. The following table shows the differences in soil moisture at different depths over the growing season in the forest soil as compared with the denuded soil. The forest was a fully stocked stand of white pine, 60 years old. The moisture content is expressed in percentage of the volume of soil in place.

AVERAGE SOIL MOISTURE AT DIFFERENT DEPTHS DURING THE GROWING SEASON IN THE FOREST AND IN THE OPEN

Depth in Centimeters	Denuded Site	Forest Site
0–10	20.7	14.4
10–20	24.2	16.1
20–30	20.1	13.0
30–40	13.2	8.4
40–50	9.2	6.9
50–60	8.5	6.3
60–70	8.1	4.9
70–80	9.5	4.7
80–90	8.4	4.5
90–100	8.3	4.7

Craib (1929) has shown that, in fully stocked stands of white pine in New England, the moisture in the soil layers immediately below the litter, and often down to a depth of one or more feet, may be reduced below the wilting coefficient during periods of prolonged drought. It is this reduction in available soil moisture, owing to density of the existing stand, that inhibits development of vegetation on the forest floor. It appears to be the severe competition for soil moisture and nutrients that eliminates subordinate layers beneath a dense overstory in many upland forests.

Upland forests on slopes and ridges in New England, where the overstory forms a dense, continuous canopy, are often without subordinate layers, yet stands in ravines and at the base of slopes, with even denser canopy in the overstory, have well-developed subordinate layers. In the latter stands, soil moisture apparently does not become critical.

Vertical zonation in forests and the presence or absence of subordinate layers appear to be largely a response to soil moisture in most forest regions.

Toumey and Kienholz (1931) have shown that trenched quadrats in white pine forests, entirely without subordinate layers, soon become covered with vegetation. So long as root competition for soil moisture and nutrients is controlled, no pine stands have been found with a canopy sufficiently dense to inhibit the development of subordinate layers. Quadrats 9 feet on a side were established in stands of white pine without subordinate layers and with a continuous litter of pine leaves. One-half the quadrats were trenched, and the remainder were held as checks. The roots from the trees were severed at times of trenching in order to keep them from entering the trenched quadrats. In every case, irrespective of density of canopy, abundant vegetation appeared in the trenched quadrats, because the soil had been freed from living roots of surrounding trees. On the other hand, little or no vegetation appeared in the check quadrats (Figs. 11, 12, and 13).

Working with the same quadrats, Craib (1929) found that the amount of available soil moisture is greatly increased by elimination of root competition. During dry periods two to nine times as much moisture available to plants occurred in the first 6 inches of soil in the trenched plots as in the untrenched plots. He reports that more moisture is usually available in the surface soil layer than at increased depths, which helps to explain the prevalence of roots of forest vegetation in the uppermost foot of soil. During the driest periods of the year, which may occur any time during June, July, August, or September, the amount of available soil moisture in a forest sometimes falls below the minimum amount necessary to sustain life of the lesser vegetation. This fact is of great significance in accounting for lack of survival of reproduction beneath dense forest canopies.

Results of trenching experiments comparable to those of Craib (1929) and Toumey and Kienholz (1931) were obtained in the loblolly pine, shortleaf pine, red gum-yellow poplar, white oak-black oak-red oak, and post oak-blackjack oak forest types of the North Carolina Piedmont plateau. The trenched quadrats contained a significantly greater amount of soil moisture than their corresponding untrenched

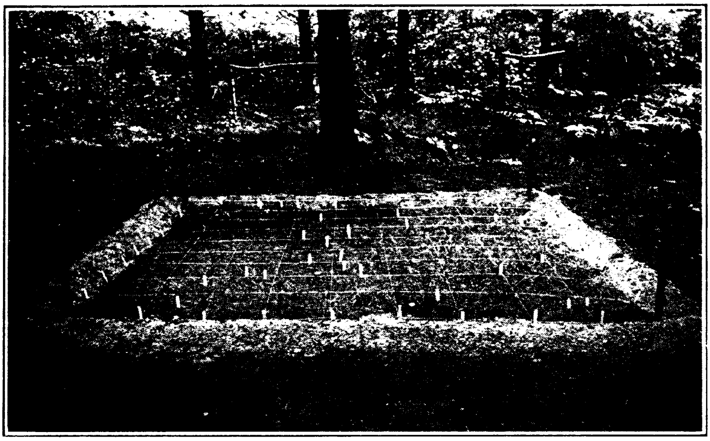


FIG. 11. — A trenched area with untrenched areas at either side under a white pine stand 45 years old. Photograph taken immediately after trenching. Note the meager vegetation on both the trenched and untrenched areas.

FIG. 12. — The same areas as in Fig. 11 but photographed one year after trenching. Note abundance and vigor of herbaceous vegetation in the trenched quadrat as compared with that in untrenched areas.

quadrats every growing season since establishment, their vegetation has already become denser, and additional species commonly inhabiting moist situations have appeared (Korstian and Coile, 1938).

8. Absorption of Soil Water by Trees. — The absorption of water by trees is closely related to transpiration and certain other physiological processes. Transpiration sets in motion the forces which bring about moisture absorption by transpiring trees. The cohesion theory, which involves the cohesion and tensile strength of water in explaining the ascent of sap in trees, indicates how the forces produced in the tree tops by the loss of water from the leaves in transpiration can be trans-

FIG. 13. — The same areas as in Fig. 11 five years after first trenching. Note abundant, vigorous reproduction of hemlock, white pine, gray birch, aspen, and other trees in the trenched quadrat, and their complete absence in adjacent untrenched areas.

mitted through the water in the xylem to the roots and there bring about water absorption. Kramer (1945) explains that the evaporation of water from the mesophyll cells of the leaves produces a deficit which causes water to move into these cells from the xylem of the leaf veins. Thus removal of water by transpiration decreases the pressure or causes tension on the xylem sap, producing a gradient of decreasing pressure along which water moves from the epidermis of the roots to their xylem and on to the xylem of the stem, branches, and leaf veins. The roots act essentially as passive absorbing surfaces in this process, relaying to the soil solution the forces set in motion in the leaves by transpiration.

The rate of water absorption by trees growing in moist soil is influenced markedly by the rate of transpiration and by the factors affecting it. The absorption rate is also influenced by the extent and efficiency of the root systems. Important environmental factors affecting water absorption are the available soil moisture, the concentration of the soil solution, soil aeration, and soil temperature (Kramer, 1945).

9. WATER SUPPLY OF FOREST SOILS

The actual water content of soil is the difference between that supplied and that lost. Although it varies in different soils and under different conditions, all ordinary forest soils when well drained tend to maintain their water content within fairly definite seasonal limits. At times of overly abundant precipitation the excess or gravitational water soon drains away and the remainder gradually and slowly becomes reduced through evaporation and by transpirational loss from vegetation. This reduction continues until more water is supplied, chiefly through precipitation, when the process is repeated. The supply is intermittent, and the loss is more nearly constant. The process of slow reduction, although it may not be excessive, measured in the amount of water withdrawn, is of far-reaching importance in its bearing on vegetation.

The actual amount of water in a given forest soil, being the difference between that supplied and that lost, depends on the nature of the supply, on the forces operating on soil to withdraw it, and the resistance which soil offers to these forces. The consumption of water by different types of vegetation varies between wide limits; consequently vegetation, to no small degree, determines the rate of withdrawal. This has been a matter of considerable inquiry and physiologists have in many cases determined the amount of dry matter produced per given volume of water taken from soil and have called this the *transpiration coefficient*. There appears, however, to be no constant relationship between transpiration and assimilation, the coefficient varying with temperature, nutrient supply, and many other factors.

In general, the amount of dry organic matter capable of being produced on a given area of forest soil increases with increase of available water up to a given point, when yield falls off owing to gravitational water's restricting the air supply for roots. When the supply of available water is less than the optimum, qualitative differences are revealed in form and habit of root system and in form and color of parts above ground, particularly leaves. There may also be differences in chemical

composition. Water in excess of the optimum may not only restrict aeration but it is also likely to occasion formation of reduction products which may have toxic effects on vegetation.

Available water in the soil depends not only on the interplay of physical forces which measure the extent to which vegetation present can withdraw the water held between the soil particles but also on the relative purity of the water which determines whether it can be withdrawn at all. Other things being equal, roots withdraw much more water from soil when the water reaches them in a relatively pure condition. There appears to be a limit to the degree of concentration of salts and other substances in soil water beyond which osmosis is inhibited, and the roots are no longer able to absorb water. According to Schimper (1903) the concentration rarely exceeds 5 percent. Species which grow in saline soils in arid regions and along seashores are able to absorb little water, as evidenced by their xeromorphic structures. Most arborescent species are excluded from soils which carry an excess of salt, because of lack of usable water. Practically all upland forest soils, however, and particularly those that are well drained, are free from an excess of salts and other substances that interfere with absorption.

Soil toxins appear to inhibit absorption in certain instances, and the colloidal nature of the soil solution in acid soils appears also to restrict absorption (Rigg and Thompson, 1919).

When a given species is no longer capable of extracting water from a given soil, although a large quantity may be present, that soil is physiologically dry for that species (Warming, 1909). It is the physiological dryness of a soil and not its physical dryness which determines the growth forms which appear in forest vegetation.

The more the water in a given soil decreases in amount, the more firmly held is that which remains. In all soils a point in withdrawal of water is finally reached at which tree roots can not absorb enough to keep the above-ground parts from wilting, although a relatively large amount may yet remain in the soil. Sachs (1865), by a carefully executed series of experiments, demonstrated great variation in different soils in the amount of contained water unavailable for vegetation.

Experiments have shown that water may be reduced in a coarse, sandy soil to only 1.5 percent of its dry weight, before a plant growing in it begins to wilt; but the same species growing in loam may begin to wilt when the water is reduced to 8 percent, and in peat, when reduced to about 47 percent.

During recent years much attention has been given to wilting and to the relations of atmospheric conditions to the amount of water left in soil at the wilting point in various plants. From the experiments of Briggs and Shantz (1912) and others, much definite knowledge has been gained relating to water intake of plants under different soil moisture conditions. The capacity of a soil to supply water to the absorbing roots of a plant depends upon temperature, texture, and structure of soil and its water content per unit volume of soil. A soil with water content equal to or only slightly less than its maximum field capacity can supply water at a rapid rate. This rate steadily decreases as a soil becomes drier through absorption of water by plant roots and through evaporation into the air (Livingston and Koketsu, 1920; Wilson and Livingston, 1932). When the water-absorbing capacity of plants becomes greater than the effective water-supplying capacity of the soil around the absorbing roots, incipient drying becomes so pronounced that the growth of plants is retarded or checked. The wilting of plants at the wilting percentage is directly due to the slowness of water movement from soil particle to soil particle and from these to the root hairs. As a soil becomes drier the rate of movement falls below that necessary to maintain turgidity in the cells of the aerial parts, even under conditions of low transpiration. If drying continues, permanent wilting may follow. At permanent wilting the water-supplying capacity of soil is the same for different soils within certain limits. The amount of water left in any soil, when plants rooted in it wilt permanently, is a function of the intensity of atmospheric evaporation for the period preceding permanent wilting (Caldwell, 1913; Shive and Livingston, 1914).

10. Fluctuations in Available Water in Forest Soils

The character of vegetation is determined not so much by average amount of available moisture in a soil as by amount of moisture at the driest periods during the growing season. All soils immediately after heavy rains carry water in such excess that it freely flows from them without pressure. At the driest period of the growing season, however, there is great variation in the water content of soils under uniform climatic conditions, depending upon location, particularly with reference to aspect and slope and upon condition of the surface. Water content also depends on depth of soil and on its physical and chemical nature.

11. INFLUENCE OF AVAILABLE SOIL MOISTURE ON FOREST VEGETATION

Although every *species has certain soil moisture requirements under which it does best*, there is a wide range in different species in the variations in available soil moisture under which each will thrive. The vigor and growth of a given tree depend largely upon how nearly the conditions conform to the maximum soil moisture requirements for the species to which it belongs. White pine, red maple, and slippery elm occur under a comparatively wide range of soil moisture conditions. Yellow and river birches and southern white cedar are restricted to soils in which the available soil moisture falls within much narrower limits.

In nature each species is adjusted both in form and structure to its normal water requirements. External factors which determine absorption and loss of water may react upon trees so as to change their form and structure and by so doing favor or impede entrance or exit of water. These changes are so pronounced that they very largely determine the character and form of forest growth. The physiognomy of a forest is often largely determined by the available water supply. Furthermore, available water may determine the presence or absence of forest growth. Evidence on influence of water in limiting the occurrence of forests may be had from the studies by Bates (1924) in Colorado, Pearson (1931) in the Southwest, and by Baker and Korstian (1931) in the Intermountain region. Soil moisture is generally much more abundant in the Engelmann spruce and Douglas fir zones than in the lower ponderosa pine and piñon-juniper zones. Variations in the combination of factors which influence soil moisture directly or indirectly, such as temperature, soil texture and structure, physiography, and the presence of competing vegetation, explain many of the causes underlying the failure of forest plantations to survive and develop satisfactorily on many areas in the Intermountain region (Korstian and Baker, 1925; Baker and Korstian, 1931). Clements, Weaver, and Hanson (1929) conclude that water is of paramount importance in competition within the tension zone between broadleaf forest and prairie. Forests give way to lesser forms of vegetation, such as grassland and desert, when available water supply falls too low. There is, however, no place on the earth's surface that, where the soil itself is not completely submerged, the water supply is too great to sustain some type of forest.

Available soil moisture holds a commanding place in accounting for distribution of forests and particularly their local occurrence. In the

process of development some species have become adjusted to dry habitats; other species have become adjusted to wet habitats. Their moisture endurance is also reflected in their form and structure. Between these two extremes are all degrees of form and structural variation, depending upon the combination of all external factors which, working together, reduce absorption by roots and increase transpirational loss through shoots.

The capacity of plants for enduring drought, or their drought resistance, depends upon the relative efficiencies of their mechanisms for increasing absorption and conduction and for decreasing transpiration as compared with the normal balance between their water intake and water outgo. Drought resistance of many species is reflected in their physiological functioning, form, and structure. Magistad and Breazeale (1929) conclude that rapidity of absorption of plant nutrients is largely a function of concentration of nutrient solution and that with some plants, at least, water moves either from soil to plant or from plant to soil, depending upon the nature of the moisture gradient. Breazeale (1930) goes so far as to say that a plant may absorb moisture from any soil horizon where water is available, for example the subsoil, and transport this moisture to another horizon where moisture is scarce, for example the surface soil. It may there exude this water, dissolve and absorb certain amounts of nutrient materials, and thus maintain its equilibrium, at least within certain limits. Thus Breazeale and Crider (1934) conclude that the roots of certain plants are able to penetrate soils the moisture contents of which are below the wilting point. They even point out that a certain amount of dependence of one plant upon another may exist in nature with reference to their moisture supply; that is, a deep-rooted plant may absorb moisture from the subsoil, transport it, and exude it into the surface soil where a shallow-rooted plant may absorb it and thus tide over periods of stress.

Pearson's (1931) experiments with blue spruce, Douglas fir, ponderosa pine, and limber pine have shown that when soil moisture approaches the wilting percentage all these species reduce transpiration almost to zero; and yet they can persist in this condition for months at a time.

There is little or no correlation between the taxonomic relationship of species and growth form (Warming, 1909). Many arborescent species of cacti and certain Euphorbias, though widely separated taxonomically, are almost identical in growth form. On the other hand, upland trees are often in the same family with such widely divergent growth forms as aquatic plants, vines, and climbers. Drude (1896) has

classed the growth forms of lignified plants with long-lived stems under:

1. Canopy trees.
2. Shrubs.
3. Dwarf shrubs.

The evolution of growth forms under identical environmental conditions does not always follow the same trend. Thus one species may adjust itself to a site with little available moisture by a more or less dense covering of hairs, as in sagebrush of the western United States. Another may attain the same position by a coating of wax over the transpiration surface, as in creosote bush, or by a reduction in foliage and the development of a succulent stem, as in giant cactus. The natural adjustment of trees to their water requirements is such that each species can attain its maximum development only on sites where moisture conditions fall between relatively narrow, though ill-defined, limits. No tree reaches its maximum development on both dry and wet sites. With every species, a deviation from the limits in either direction causes a marked decrease in vigor or growth, or in both. Finally if the deviation in either direction is carried too far a tree can no longer survive.

12. Adjustments to Available Soil Moisture

As the supply of water available to a tree and the regulation of evaporation work together in causing differences in growth form, adjustments in shoots for the most part relate to outgo of water, and those in roots relate chiefly to water intake. Transpiration is a physiological process determined by both external and internal factors. The external factors are evaporation, which influences the parts above ground, and available soil water, which influences the parts below ground. Evaporation, however, by affecting soil conditions, also influences the parts of trees below the surface (Clements, 1904).

The internal factors which control outgo of water relate to the nature, area, and position of the transpiring surface; those that control the intake of water relate to the nature, area, and position of the absorbing surface (Warming, 1909).

All species of trees are able to occupy a greater variety of sites near their centers of geographical distribution, owing to the influence of compensating factors. In the process of reaction under various site conditions, some of the new structures, habits, and forms which arise are advantageous, some disadvantageous, and others indifferent. After variation takes place only those variations are likely to survive that are

suited to the site where they arise. The others, through natural selection, are likely to disappear. This is the reason why a preponderance of advantageous structures, habits, and forms occur in nature and why trees appear to be more or less closely adjusted to their particular habitat. Regarding water loss and water intake of trees, natural selection has retained in the progress of evolution the structures, habits, and forms in each species that are useful in providing it with adequate water under its particular environment.

13. Adjustments for Control of Water Loss

The main responses of the parts of trees above ground, tending to control the loss of water, are the result of variations in:

1. Internal structure.
2. Area of evaporating surface.
3. Illumination of assimilating organs.
4. Epidermal outgrowths and coverings.
5. Shoot form, particularly in height growth.

The resistance offered to water loss is extremely variable. In general, however, the rate of loss from the transpiring area is many times lower than that from an equal area of water surface in the same surroundings. The resistance is of different magnitude for different growth forms and for the same form under different conditions (Livingston, 1913). The factors which bring about the retarding influence operate within a tree but are controlled by present or past external conditions. An appreciation of the dynamics of water relations of trees necessarily rests not only upon a quantitative knowledge of the influence of external factors on transpiration rate but also on a knowledge of the relations which exist between rate of water loss and the internal factors which control it.

14. Variations in Internal Structure. — Water loss by transpiration takes place through the epidermal cuticle and through the stomata. The variations in structure which control water loss through the cuticle of leaves and branches are diverse. Thus in water plants the cuticle is as a rule thin and permeable, but in dry-soil plants it is usually thick and more or less impermeable. Warming (1909) states that various substances, such as tannins, in the epidermal cells may render them less permeable to water vapor. The development of mucilaginous cell walls in the epidermis may, according to Volkens (1890), check transpiration. The formation of cork and bark tissue effectively checks loss of water from the main axis and its branches. Cork tissue is more

highly developed in desert and upland trees than it is in species that inhabit regions physiologically moist.

In general, trees which attain their maximum development on a site having an abundance of available soil moisture have thinner bark than trees which reach their maximum development where there is little available soil moisture. Swamp and lowland species usually have thinner bark than upland species. The thin-barked species, red maple, sycamore, yellow birch, black ash, and beech, occur in moist or wet soils. The thick-barked species, chestnut, chestnut oak, and post oak, occur on dry upland soils. The cork development of white elm, a lowland species, is much less than that in rock elm, a species of dry uplands. So also when the inner walls of the respiratory cavity are cutinized, as in many species adjusted to dry soils, loss of water through the stomata is much reduced. Other structural variations which regulate water loss through transpiration are exhibited in the greater development of vascular and sclerenchyma tissue and in water storage tissues in species adapted to dry soils.

Variations in structure that control water loss through the stomata are also numerous. All stomata with mobile guard cells are regulators of transpiration. They close as plants wilt and open with increased turgor. Often stomata in plants growing in habitats physiologically dry are sunken beneath the leaf surface in pits or furrows protected by hairs. The cavities beneath the stomata and intercellular spaces also regulate water loss through the stomata. When the spaces are small there is less loss of water.

15. Variations in Area of Evaporating Surface. — The area of evaporating surface plays an important part in determining water loss through transpiration. Other things being equal, water loss is directly proportional to area exposed. The area of transpirational surface is in most species variable, depending upon the season. Thus many trees reduce transpiration by shedding their foliage during dry and cold seasons. The leaves of evergreen species are usually much thicker and more resistant to water loss than those of deciduous species. The paloverde of Arizona usually sheds its leaves shortly after blossoming in the spring and puts forth new foliage during the summer rains of July and August. Most deciduous species are strikingly xerophytic except in the growing season. As leaves are present only during the most favorable season, they are usually without such strongly developed xeromorphic structures as are characteristic of evergreen species. The reduction in area of foliage exposed to the air is sometimes attained by the rolling or folding of leaves with an increase in evaporation.

They assume their normal position with a reduction in evaporation.

Trees not only vary their transpiring area with the season, as in all deciduous species, but there is a permanent reduction in the transpiring area of species adjusted to soils that are physiologically dry during more or less extended periods in the growing season. Thus in giant cactus of Arizona the foliage is completely eliminated; and in many other species of cacti it is greatly reduced in area, owing to the small size of leaves.

16. Variations in Illumination of Assimilating Organs. — Some tree species orient their foliage in response to light (Darwin, 1881). When light intensity is low, leaves are oriented so that the rays strike them at or nearly at right angles. As light intensity increases they assume a position in which they lie more and more parallel with the light rays and therefore receive less illumination and heat. As transpiration is increased by solar radiation this response of certain leaves to light intensity has the effect of reducing water loss through the foliage.

The foliage of most tree species during the process of early development assumes a position in which the blades of leaves are permanently placed perpendicular to the light of greatest intensity, as in beech, oak, maple, and most hardwood species of mesic habitats in temperate regions. Some species, however, as in certain species of eucalypts, expose their edges toward the greatest light intensity or assume a more or less erect position, as in mangrove (Schmidt, 1905). Wells and Shunk (1931) have reported a notable case of turkey oak in the sandhills of the Carolinas, in which juvenile leaves are naturally oriented in a plane perpendicular to the ground surface. When artificially held in a horizontal position during a moderate drought they were injured. In general, the position that foliage leaves assume is the one generally most favorable with reference to light (Wiesner, 1876). Water loss, however, is necessarily affected by the position assumed.

17. Variations in Epidermal Outgrowths and Coverings. — When the transpirational surface is more or less densely covered with epidermal hairs or other trichome structures which are dead and contain air, free circulation of air is checked adjacent to the epidermis and as a consequence transpiration is materially reduced. It is a matter of common observation that species with glabrous surfaces, such as black gum and red maple, are more characteristic of wet areas. On the other hand, species with hairy coverings, such as many upland oaks, are more abundant on dry areas. Warming (1909) states that some species which are glabrous in moist habitats become covered to a greater or less degree with pubescence or other trichome structures in dry habitats.

Epidermal outgrowths, such as hairs, are usually most abundant on the lower surface of leaves, where, because of stomata, there is the greatest water loss.

18. Variations in Shoot Form, Particularly in Height Growth. — A number of arborescent xerophytes, such as species of *Canotia* and *Koeberlinia*, indigenous to Arizona and New Mexico, are without foliage leaves. Their function has been taken over by the main stem and branches, which are green in color, with stomata and palisade tissue. Other species of the same general locality, such as some of the arborescent species of *Dalea* and *Parkinsonia*, have leaves greatly reduced in size and depend chiefly upon green branches for photosynthesis. Sometimes where leaf function is transferred to the stem, the stems become more or less flattened or angular.

A correlation appears to exist between height growth of trees and available water supply. A decrease in the water requirements for optimum growth results in a rapid falling off in height growth. A deep soil which contains an abundance of moisture during the growing season results in optimum height growth for the species. Thin soils in which there is a scanty supply of moisture during the growing season produce trees of low height for the species (Coile, 1935). Thus on the deep, well-watered soils of our eastern hardwood forests, the trees as a rule are a third to half taller at maturity than the same species when growing on the thin soils of steep slopes from which a large part of the precipitation escapes as surface runoff. Dry soil and high evaporation cause trees to assume a characteristic stunted habit.

19. Adjustments for Control of Water Intake

The chief responses of parts of trees below ground tending to control water intake are due to variations in:

1. Internal structure.
2. Sap density.
3. Area of root surface in proportion to shoot surface.
4. Root habit and root form.

20. Variations in Internal Structure. — Water enters the subterranean parts of trees, which usually branch freely and penetrate the soil in all directions, through the entire absorbing surface. The absorbing surface is very greatly increased by the extension of epidermal cells into root hairs. Most living epidermal cells in roots have capacity for developing root hairs, although the hairs are often absent. The chief function of root hairs is to increase the permeable surface of roots which

may be 5 or even 10 times that of hairless roots of equal size. As root hairs are ephemeral structures that are continually arising just back of the root tips during the growing season and are constantly dying, a migration of root-hair zones progresses into new soil areas from which water has not been exhausted through absorption by roots.

All roots in most tree species serve for both absorption and anchorage. In some, however, as in many cacti, there are a number of descending anchorage roots and also a number of horizontal nutritive roots which are more or less clearly differentiated structurally (Preston, 1901). The central vascular strand in typical anchorage roots is composed of thick-walled cells of small diameter. On the other hand, in typical absorption roots, it is composed of thin-walled cells of relatively large diameter. Species adapted to arid habitats often have root hairs with lignified walls, as illustrated in nut pines (Coulter, Barnes, and Cowles, 1930, 1931).

Very early in the life of roots, and soon after root hairs disappear, the entire epidermis is eliminated and the exodermis becomes the outer layer of roots. The degree of cutinization of this layer determines its capacity for absorption. Although root systems are more or less extensive and ramifying, with a large superficial surface, the absorption area in all species is chiefly the root terminations that lie beyond the exposed exodermis. Many species indigenous to arid soils develop a thick cortex over the roots with the exception of the absorbing surfaces. This cortex protects the living tissue beneath from dry soil during periods of drought (Masters, 1891; Kunkel, 1912; Cannon, 1913; Hayden, 1919).

21. **Variations in Osmotic Pressure of Sap.** — The absorption of water and of substances in solution by roots is practically the only method by which trees obtain nutrients from soil. This passage of water through a tree is not a simple process. Not all water-soluble substances are able to enter a tree through its root system (Jost, 1907). Water, with its solutes, must penetrate the cell walls and the layers of living protoplasm within the cells; hence the passage of water is complicated by the presence of substances already in solution in the cells. This involves osmosis or the movement of the solvent through cell-wall membranes from the weaker to the stronger solution. The laws of osmosis, as developed by Pfeffer (1877) and simplified by van't Hoff (1887) and others, show that the exchange of materials between a soil and living plant cells as well as between the cells themselves is based on the principles that a substance in solution tends to distribute itself uniformly throughout the solvent, and that no absorption will take

place when the concentration of the soil solution is equal to that within the living cells of tree roots. Furthermore, if the outside solution is the more highly concentrated, water will actually be drawn from the tree into the soil. It is only when the solution within a tree is more concentrated than the soil solution outside that water will pass through the walls of the root hairs into the living cells and from one cell to another to the foliage. A gradient of decreasing osmotic pressures has been observed from leaves at the tree tops to those at the bases of tree crowns and to the roots (Korstian, 1925).

The osmotic pressure set up by this movement is difficult to measure by direct means; however, depression of the freezing point, elevation of the boiling point, decrease in vapor tension, and osmotic pressure of solutions are all related phenomena and one can be calculated quite readily from another. As the osmotic pressure of the intercellular solute of a given tree is an index of the tree's ability to draw water from the soil when compared with the concentration of the soil solution itself, it is coming to be used in attempting to solve some of the basic physiological problems of silviculture that relate to available water supply.

Studies by Korstian (1925) suggest that determinations of sap concentration of forest vegetation might be used as indicators of site conditions. The work of Gail (1926) and Meyer (1928) indicates the possibility of relating osmotic pressure of cell sap to cold resistance. Also osmotic concentration of plant sap has been related to drought resistance. Maximov (1929), after reviewing the results of many European investigations, concludes that the possession of cell sap with high osmotic values enables many non-succulent, drought-resistant plants to absorb water from soils which have rather highly concentrated solutions, although not so concentrated as sap in the roots. A high osmotic pressure of the sap may delay visible wilting for a long time. The protoplasm may be protected from desiccation and, sometimes from coagulation, as the result of accumulation of sugars and other substances which incidentally cause high osmotic concentrations. Even in the mesophytic forest on the Piedmont plateau of North Carolina, preliminary results indicate that the species which are relatively more drought-resistant usually have a higher osmotic concentration coupled with a lower total water content in the leaves, a higher percentage of solids, and a higher percentage of water which is bound by hydrophyllic colloids (Korstian, 1933).

22. Variations in Area of Root Surface as Compared with Shoot Surface. — The relative proportion of surface exposed below ground

as compared with that exposed above ground is variable in different species. As a rule, roots of species adjusted to dry soils are extensively developed in comparison with the parts above ground. The larger and more extensive the root system in proportion to the shoot, not only the greater the asborption surface but the more likely is root contact with remote supplies of water. Although extensive root development, compared with shoot development, is characteristic of dry soils, some plants of very dry soils have relatively small root systems. This is true of various cacti and other plants which have the power to absorb water in excess of their needs when it is abundant in the soil and conserve it in special storage tissue for use when required later for transpiration and growth. Devices for storing water are frequently found in xerophytes but are lacking in other species. In contrast with most dry-soil plants, with their relatively extensive root systems, are swamp species with their meager root systems in proportion to their tops.

23. Variations in Root Habit and Root Form. — The geotropic tendency of roots is usually favorable for both absorption and anchorage and is most evident in taproots. Lateral roots branch in all directions. If a taproot is removed, one or more of the lateral roots often bend downward and assume its position. Although gravity causes roots to grow downward, water exerts an even stronger influence and may overbalance the force of gravity. Thus roots usually grow into moist soil areas even when thrown out of vertical in doing so. The downward growth of roots is arrested by the presence of free water in soil, except in a species occurring naturally in swamps. McQuilkin (1935) reports that pitch pine is capable of extensive root growth in saturated soils below the water table. Southern white cedar and its associates commonly grow in peat swamps which are inundated or saturated with water during much of the year (Korstian and Brush, 1931).

It is well known that many plants of arid regions, such as mesquite, possess deeply descending taproots which aid them in obtaining water at great depths during long periods of drought. Volkens (1887) states that some desert species develop roots twenty times as long as the shoot above ground.

Hilgard (1906) has shown that in arid soils of California the main roots of figwort and goosefoot, two common perennial weeds, often penetrate heavy black adobe soil to a depth of 10 or 11 feet. The senior author observed the roots of mesquite near Tucson, Arizona, which attained a downward soil penetration of 28 feet, or more than twice the height of tree above ground. A 3-year-old sugar pine was found by

the same author in the Sierras of California to have a root penetration of 6 feet, or 18 times the length of the shoot.

Not all species of arid regions have deeply penetrating roots. Many species that grow on upland soils in the arid Southwest have comparatively shallow roots, as pointed out by Cannon (1911), and those growing on floodplains have deeply penetrating ones, owing to their correlation with ground water available at some distance below the surface.

Although not all trees are deep-rooted when growing in arid soils, all species that naturally occur in such soils are comparatively deep-rooted in their early life. Trees that attain a root penetration of but 4 to 8 inches during their first year's growth are never found in arid soils. Species indigenous to dry soils almost invariably attain a root penetration of 12 to 30 inches the first year. Only those species with a rapidly developing and a comparatively long initial root survive in dry soils; on the other hand, a rapidly developing, long initial taproot is not essential for survival in moist soils. Soil type greatly modifies root form of ponderosa pine seedlings (Haasis, 1921).

24. Variations in Root Habit as Expressed in Adult Trees. — Although there is more or less variation in form and habit between individuals of a given species, due to differences in available soil moisture, variations are much more pronounced in adult than in juvenile plants. Change in root habit within a species, variety, or race, brought about by change in water content, is scarcely perceptible in the early seedling stage, but becomes more and more pronounced with age. Thus sugar pine grows in a region having a long period of summer drought and has a deeply penetrating initial root. Seeds of this species when sown in regions where surface soil is uniformly moist continue to produce the same type of initial root. Later the root system becomes much modified, depending upon available moisture and other soil conditions. There is, however, great variation in different species in the early adjustment of a root system to a change in soil moisture conditions. Species like red maple, paper birch, and slippery elm have much more adaptable initial root systems than species like hickory and most oaks.

25. Plasticity in Initial Root System. — Although the root habits of a tree are governed primarily by hereditary growth characteristics of the species, they are often quite as much the product of environment (Weaver, 1919; Weaver and Kramer, 1932). When red maple becomes established in dry soils, the initial root system is almost from the start different from what it is when germination takes place in swamps. In this species the initial root system is extremely plastic. Almost from

the beginning it is short and spreading on wet soil, rarely reaching a depth of more than 2 to 3 inches the first season. In dry upland soil the primary root continues its downward growth throughout the entire season, often reaching a length of 10 to 13 inches. In wet soil lateral roots are abundant and well developed; in dry soil they are relatively unimportant. This species is capable of adjustment for early growth under a wide range of soil moisture conditions. Although commonly found in swamps, it is frequent on dry upland where the surface soil is far too dry for yellow poplar or walnut. The generalized root system of boxelder is also very plastic (Biswell, 1935). In dry upland soils the taproot and most of the branch roots penetrate deeply; in moist alluvial soil the root system is much shallower but extends widely in the surface foot of soil.

In most tree species the inherent juvenile root habit is not essentially modified by external conditions. Pignut hickory, under all conditions of available soil moisture, has the same type of initial root. Even mechanical obstructions in the soil or the removal of the taproot will not induce the development of strong lateral roots during the period of early growth. Species in which the initial root system is plastic, as in red maple and boxelder, occur on sites varying in available soil moisture and are likely to exhibit a large variety of habitat forms. Species, such as pignut hickory, red cedar, and chestnut, that have non-plastic initial root systems of great length, are characteristic of dry upland soils. They often occur, however, on low moist land, but on such sites they never become the dominant trees because they can not compete with other species of more rapid initial upward growth and more shallow, spreading initial root systems, which, particularly in early life, are far better adapted to sites with moist surface soil. When competition is removed, species with deeply penetrating initial roots can become established on sites where the superficial soil layers remain moist throughout the year. Species like southern cypress and yellow birch that have short, non-plastic initial root systems are never established through natural seeding on sites where the surface layers of soil become dry during the growing season.

In the later development of root systems in species with non-plastic initial roots more or less variation occurs, depending upon the varying influence of site factors. No matter how great this variation may be, however, for all practical purposes the line of descent is brought back to its original form through seedlings. In the early life of a tree there is an inherent tendency to develop a root system similar in downward growth and form to that of the seedling form of the parent plant.

26. Correlation Between Rapidity of Juvenile Root Penetration and Surface Desiccation of Soil. — In their early life young trees draw their supply of moisture from more or less superficial soil layers. Later, moisture is also obtained from greater depths. The surface layers of soil are in all regions subject to excessive variations in water content, largely because of irregularities in precipitation and loss through evaporation; the deeper layers, being below the immediate effect of precipitation and evaporation, have a much more uniform water supply. In order that a tree may start its growth and survive in any region, the early downward growth of roots must keep pace with the loss of moisture from the superficial layers of soil during periods of drought. Hemlock, spruce, and beech in the early seedling stage thrive under the protective shade of an overstory because of the effect of the canopy on moisture conditions of the surface layers of soil. Where they germinate in the open, the downward growth of roots is not adequate to keep pace with the natural desiccation of the surface soil. On the other hand, hickories, oaks, and many pines thrive when exposed to full sunlight from the very first. In these cases the downward growth of roots is sufficiently rapid to keep ahead of the desiccation of the surface layers of soil.

27. Depth of Root Penetration in Relation to Available Soil Moisture. — In general it may be said that the ability of a given species to persist on a particular site or to become established in a new region depends very largely upon its initial root habit and how closely it is correlated with available soil water from which it draws its supply. Because of the great differences in the initial root habit of one species as compared with another, particularly in relation to rapidity of downward growth, the moisture available for one species may be very different from that for another, even when both are growing in the same soil. Thus trees with marked xeromorphic structures are often found growing in the shade of mesophytes. On leached, loose shales of eastern Pennsylvania, forests of oaks and hickories have a more or less dense undergrowth of ericaceous shrubs, all having characteristic xeromorphic structures. The soil is so coarse and permeable that the precipitation rapidly passes from the surface to the deeper layers and that which remains is largely lost through evaporation. The species with mesomorphic structures are deep-rooted while those with xeromorphic structures are shallow-rooted. Oaks, chestnuts, and hickories develop roots which reach a depth of 15 to 30 inches the first season. They very early attain a depth which gives them an adequate water supply even during periods of prolonged summer drought. On the other hand, the

xerophytic undergrowth has roots which penetrate the soil only to the depth of a few inches, and consequently during periods of drought much less moisture is available to them.

The concentration of tree roots in the *A* horizon of most forest soils indicates the need for an immediate aerial source of soil moisture rather than vertically or laterally translocated moisture (Coile, 1936).

28. Characteristic Forms of Initial Root Habit and Their Relation to Available Soil Moisture. — Because of great variations in moisture conditions of the superficial soil layers and the necessity for compensation between water loss and water supply of the plant, a root must quickly reach a position in the soil where it is able to meet the demands of a particular species for water to sustain transpiration and growth. In order to do this the root habit must be correlated with the tendency in any particular soil toward downward desiccation.

The depth and form of root system of hardwood trees appear to be correlated with water content of soil; the long taproot with strong branches is characteristic of species adapted to drier sites (Holch, 1931).

There are two extreme forms of initial root in woody plants (Toumey, 1929). These forms are based on rapidity of downward growth and consequent depth of soil penetration during juvenile growth. At one extreme is the deeply penetrating initial root without prominent laterals and at the other the short initial root with numerous widespreading laterals. Every variation in depth of root penetration and width of lateral expansion is found between these two extreme forms, depending chiefly on available soil moisture and the moisture requirement of a particular species.

29. *Species with Long Initial Taproots and without Prominent Laterals.* — The deeply penetrating juvenile root is characteristic of species that grow in desert regions, in regions having long periods of summer drought, and in humid regions where the soil is coarse, porous, and non-retentive of moisture. In general it is characteristic of all regions where the surface layers of soil are likely to become excessively dry during the growing season (Fig. 14).

The singleleaf piñon pine develops an initial root which attains a depth of 8 to 10 inches before the cotyledons have pushed out from the seed coats. By the end of the season the root often penetrates the soil to a depth of 20 to 24 inches, but the shoot is rarely more than 2 to 3 inches in length. The region of optimum growth and frequency of this species is on the low mountain slopes of southern California, adjacent to the Mojave desert. Sugar pine, an abundant species of the Sierra

Nevada Mountains of California, a region of prolonged summer drought, develops an initial root which penetrates the soil to a depth of 18 to 26 inches during the first season, and the shoot attains a height of 2 to 3 inches. Red cedar thrives in the dry, exposed soils of Connecticut and reproduces in abundance where, through exposure to wind and sun, the surface soil dries rapidly. The growth of the root after germi-

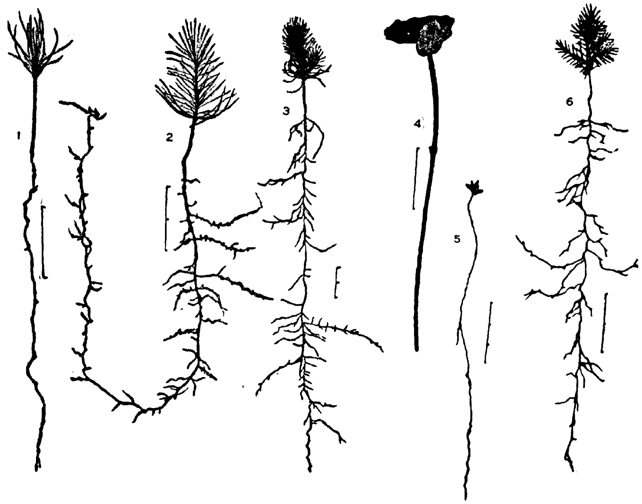


FIG. 14. — Illustrating initial root habit with long, rapidly growing taproot and with relatively few laterals. 1. Sugar pine, 6 weeks after germination. Note that there are no lateral roots. 2. Sugar pine, 10 weeks after germination. Note the numerous, but short and weak lateral roots. 3. Sugar pine, at the termination of the first growing season. Note that the most vigorous lateral roots were 8 or more inches below the surface of the soil. 4. Mesquite, 1 week after germination. Note the complete absence of lateral roots. 5. Mesquite, 4 months after germination. Note the great length of the taproot in proportion to the length of the shoot; also the almost complete absence of lateral roots. 6. Eastern red cedar, at the termination of the first growing season. Note the great length of the taproot and the relatively weak laterals. All seedlings were grown in the same seed bed at New Haven as those in Figs. 15 and 16. Divisions of scale — one-half inch.

nation is at first very rapid, often reaching a depth of 8 to 11 inches in 8 weeks after germination. At the end of the first season shoots average but $1\frac{3}{4}$ inches in height, but roots penetrate the soil to a depth of 12 to 18 inches. Species having this form of initial root are usually capable of becoming established without the protection of an overstory

and on sites where the soil rapidly loses moisture from the upper layers.

30. *Species with Short Initial Taproots and Prominent Laterals.* — This form of juvenile root is characteristic of species which grow in swamps, in regions of well-distributed precipitation, and where reproduction takes place under the canopy of an overstory. It is found on deep as well as shallow soils and on porous as well as non-porous subsoils (Fig. 15).

FIG. 15. — Illustrating initial root habit with short taproot and numerous long, strong laterals. 5. Southern cypress, 1 week after germination. Note the short taproot and the relatively long shoot. 6. Southern cypress, 2 weeks after germination. Note the short taproot in proportion to the length of shoot and the laterals already developed at the union of root and shoot. 7. Southern cypress, at the termination of the first growing season. Note the long shoot and the short taproot, with numerous, widespreading laterals. 8. Yellow birch, 12 weeks after germination. Note the great length of the strong, numerously branching lateral roots which spread out just below the soil surface and the absence of a taproot. All seedlings were grown in the same seed bed at New Haven as those in Figs. 14 and 16. Divisions of scale — one-half inch.

Southern cypress is a typical swamp species of the eastern United States. On germination the hypocotyl elongates rapidly to a length of $1\frac{1}{4}$ to 2 inches. The cotyledons soon cast off the seed coats and at the end of the first season the shoot usually reaches a height of 6 to 10 inches. During this period of rapid growth the progress of root development is slow. At the end of the season it has penetrated the soil only to a depth of 2 to $3\frac{1}{2}$ inches. The lateral roots begin to develop in

3 to 8 days after germination, and at the end of the season they are numerous and widespreading and from 1 to 3 inches beneath the surface. The initial root system of Sitka spruce of western Washington is typical of regions having high precipitation and humidity. At the end of the growing season a few irregular lateral roots often 4 inches or more in length spread out 1 to 3 inches beneath the surface and comprise the major part of the absorbing surface. Hemlock of the eastern United States finds the best conditions for germination and early growth under the canopy of an overstory where the surface soil is protected from wind and sun by the litter on the forest floor. The downward growth of the initial root is slow and seldom attains a greater penetration than 2½ to 5 inches during the first season. Many strong laterals develop early and bring the absorbing rootlets only a few inches below the surface. Species having this form of initial root habit are capable of successful establishment on soils which, for one reason or another, hold an abundance of available moisture at the surface. Western hemlock grows in regions of heavy annual precipitation but subject to prolonged summer drought. Its initial root system is so short that the species seldom becomes established on exposed soils. Although dense stands of these seedlings germinate and begin their growth in the open following a good seed year, by August 1 they are nearly all dead.

31. *Species with Long Initial Taproots and Prominent Laterals.*— In addition to the two well-marked forms of initial root habit already mentioned, there is another which combines certain of the characteristics of the other two. In this form the initial roots are both deeply penetrating and widespreading (Fig. 16). They are characteristic of species which reach their optimum development and occur in greatest frequency on soils which, because of their physical properties and profile characteristics, have a fairly uniform available water content throughout. Such soils are necessarily deep, well-drained, and of uniform texture with moderate permeability. From the standpoint of the production of both agricultural and forest crops they are the most fertile of all soils.

Black walnut, characteristic of the fertile bottomlands of the eastern United States, illustrates this form of initial root habit. It is also illustrated in yellow poplar, which grows on similar sites. In the former species the juvenile root grows rapidly downward, often reaching a depth of 25 to 35 inches the first season. A few days after germination lateral roots begin to develop, the uppermost often reaching a length of 35 to 40 inches by the end of the season. In the latter species the initial taproot continues its downward growth throughout

the season, often reaching a depth of 12 to 18 inches. Two weeks after germination the uppermost lateral roots are often longer than the taproot.

The above species and others of similar initial root habit draw their water and food supplies very largely from the surface layers of soil, although they have a deeply penetrating taproot. They are not

FIG. 16.—Illustrating initial root habit with long taproot and numerous long, widespreading laterals. 1. Yellow poplar, 2 weeks after germination. Note the length of taproot and the early start of lateral roots. 2. Yellow poplar, 4 weeks after germination. Note that the root system already shows its characteristic initial habit. 3. Yellow poplar, 10 weeks after germination. Note the long taproot and the numerous, widespreading branching laterals, particularly those just below the soil surface. 4. Yellow poplar, at the termination of the first growing season. Note the proportion of root to shoot after the fall of the leaves. All seedlings were grown in the same seed bed at New Haven as those in Figs. 14 and 15. Divisions of scale — one-half inch.

adjusted to sites which are swampy or to those in which the surface layers are subject to desiccation. They also do poorly in shallow soils.

Not only is a knowledge of initial root habit essential in selecting a species for artificial regeneration on a given site, but as emphasized by Weaver (1919) a knowledge of development, position, and competition of roots is also indispensable in explaining the phenomena of succession. Since root position reflects soil moisture conditions, particularly when

interpreted in its community relations, a study of initial root habits of trees and their later modifications gives valuable information on the usefulness of various species for particular sites and provides an important aid in the selection of the kinds of trees that can be grown most successfully.

CHAPTER VIII

PHYSIOGRAPHIC CONDITIONS

Physiography has an important indirect effect upon forest environments, mainly through its influence upon the directly operating climatic and soil factors. The distribution and occurrence of forests are governed largely by climatic, edaphic, and physiographic factors. The climatic and soil conditions are variously affected by the indirectly operating physiographic factors: earth configuration, altitude, slope, exposure, and surface conditions.

The local or microclimate, in contrast to general climate, is largely determined by physiographic factors (Braun-Blanquet, 1932). In order to consider soil in relation to forest vegetation it is necessary to take into account not only the direct factors but also the indirect factors which affect particularly soil nutrients, soil moisture, and soil temperature and, through them, the character of forest vegetation (Russell, 1932). These indirect factors concern the soil in relation to topography and the living and dead vegetation covering the soil surface.

The fundamental importance of physiography in the study of developmental changes in forests has been emphasized by Cowles (1901) and Bowman (1914). Cowles' work has forced the recognition of physiography as the most striking indirect cause of vegetation changes. Many of the site factors, and particularly the soil factors, are, in their duration and intensity of action, due to the physiographic nature of the site. Physiography within a given climatic province, through its effect on local climate and soil, causes a variety of plant communities to develop, each of which has a more or less distinct physiognomy, as illustrated in swamp forests, dune forests, river-bottom forests, and river-bluff forests. The intimate relation which exists between the physiography of a region and the grouping of its flora is primarily due to the profound effect of physiography upon the water content and composition of the soil.

1. EARTH CONFIGURATION

The configuration or topographic relief of the land surface, the direction in trend of mountain chains, and the nearness to the sea are of great climatic significance (Rubner, 1934). They very largely determine direction from which the prevailing winds come, humidity of the

atmosphere, and amount of precipitation. Differences in rock formations, such as the difference in inclination of the strata, cause differences in vegetation, as they determine the soil water supply and the location of springs. The effect on vegetation of differences in the angle and direction of stratification is most apparent in shale and slate formations. Although the soil of valleys and coves is deeper, richer, and more productive than that on ridges and on the shoulders of hills, forest vegetation growing therein is more exposed to danger from frost, owing to cold air drainage causing the formation of frost pockets. Mountain masses usually have a more uniform soil than isolated mountains and ranges of hills. Forest vegetation on the latter is greatly influenced by the direction in which the range extends. When the outermost ridge of a mountain mass is at right angles to the prevailing winds, the interior ridges are protected. On the other hand, when the prevailing winds blow parallel with the ridges, they follow the valleys and the adjacent slopes are unprotected.

The topographic relief of a locality affects forest vegetation by favoring or hindering the uniform distribution of rainfall because of the relation between the trend of mountain ranges and the prevailing direction of rain-bearing winds. Whereas the rainfall tends to be heavier on the windward side of a ridge than on the leeward side, wind-borne snow is likely to be carried over the crest and deposited on the leeward side. The effectiveness of earth configuration in the northern hemisphere appears to increase from south to north and with altitude in mountainous regions (Braun-Blanquet, 1932). Because of the constant washing down of soil materials, lower lands adjacent to slopes, especially smaller, somewhat enclosed areas, usually have more fertile soil than the neighboring slopes. Areas close to large bodies of water have moister air and more equable temperature than more distant situations.

2. ALTITUDE

Geographic climate is very much modified by altitude. The higher parts of a region are generally more subject to lightning than the lower parts. At higher elevations solar radiation during clear weather is more intense than at lower elevations. Winds are also stronger at high than at low elevations. Temperature of the soil decreases with increase of altitude and its relative importance in connection with differences in forest vegetation probably increases greatly at high altitudes and latitudes (Shreve, 1924).

The atmosphere is less dense at higher elevations. Because of this it is incapable of absorbing and retaining as much heat. In a given

latitude a fall of 1° F. in temperature results from a rise of 300 feet in altitude. This decrease in temperature largely accounts for the greater amount of precipitation on the windward side of mountains, ridges, or hills. The lowering of temperature, however, is greatly modified by the configuration of the land and by air currents. Valleys, coves, and ravines may be more exposed to danger from frosts than the adjacent slopes several hundred feet higher in elevation. Thus, in the San Francisco Mountains, in Arizona, Douglas fir is often damaged by frost when planted in the ponderosa pine type at elevations much below its natural habitat. The reason for this is that the air, chilled by night radiation, collects within low basins which are closed to free air drainage. Tender species should not be seeded or planted on such sites. They are more likely to succeed on the adjacent slopes.

In any mountainous region it may be observed that each species of tree grows best at a certain altitude. As a mountain is ascended from the plain to the mountain top, a series of zones of vegetation is passed through, each zone with one or more particular species of trees as dominants. On moderately level land, zones of similar vegetation extend over wide areas, but on steep mountains they are usually very limited in extent, and a person may often pass from one zone to another, totally different in the main features of its composition, in a mile or even less of travel. In seeding and planting in mountainous districts it is, therefore, very essential that close attention be given to the correlation of the species planted with altitude. A species may be entirely successful when seeded or planted on a particular site, suited to its climatic requirements, and fail when attempts are made to establish it on sites 1 or 2 miles away at lower or higher elevations.

Studies made in the Bavarian Alps lead to the conclusion that altitude has a marked indirect effect on the increment and shape of forest trees. Species grown at high altitudes, even under climatic conditions similar to those prevailing over its natural range at lower elevations but farther from the equator, are quite different in form and other characteristics. Thus Honda (1892) shows from his studies that the indirect effect of the increase in elevation upon individual trees is as follows:

1. Growth in height diminishes regularly and noticeably.
2. Growth in basal area, or sectional area of the stem at breast height, does not diminish so rapidly as growth in height.
3. Total increment decreases gradually.
4. The period of development is prolonged, that is, the tree is longer in attaining its maturity.

5. The stem deviates more and more from the shape of a cylinder and tends toward that of a neiloid.
6. The distribution of increment over the various portions of a tree increases relatively from above downward.
7. The form factor at breast height becomes smaller.
8. The crown development gradually comes lower down, nearer the ground.
9. The proportion of branches and branchwood increases.

The effect of increase in elevation on entire stands is as follows:

1. The number of stems per acre increases, but the proportion of those which form the larger diameter classes decreases.
2. The mean average height of a stand decreases.
3. The total basal area at breast height does not diminish so perceptibly as the average height of a stand, but it is made up mostly of units belonging to the smaller classes of stems.
4. The total quantity of wood available as timber or fuel decreases perceptibly; hence the average annual increment of an entire mature stand becomes considerably less.
5. The proportion of small branches and branchwood increases.
6. There is a decided tendency for the growth of trees in groups instead of their being equally distributed over the whole area.

Because of the differences in growth between trees occuring at high elevations as compared with those grown at low elevations, silviculturists often must modify seeding and planting operations. A larger quantity of seed per acre should be used at high elevations, and in planting the trees should be more closely spaced.

Experiments on structural changes induced by growing plants at various altitudes have shown that plants that survive moving to higher altitudes undergo changes that make them closely resemble indigenous alpine plants (Bonnier, 1920; MacDougall, 1921). The important changes are a relatively large development of subterranean as compared with aerial parts, shortening of leaves and of internodes of stems, increased hairiness, and relatively larger development of bark and protective tissue. Leaves become thicker in proportion to their surface and are a deeper green, with more highly developed palisade tissue and a large number of chloroplasts; and flowers are larger and more highly colored.

Forest nurseries should not be located at elevations higher than actually necessary for the best growth of the species planted (Toumey and Korstian, 1942). When located at high elevations the growth of seedlings may be so greatly retarded that a period of several years is necessary to bring them to suitable size to use in planting operations. Their cost is thereby unnecessarily increased.

3. SLOPE

Slope or gradient may be defined as the angle formed by the surface of the soil with the horizontal; it indicates the relation of the surface of the site to the horizon. An important effect is the control which it exerts on runoff and drainage, and through these upon water content of the soil. Another important effect is the control which it exerts through insolation on the temperature and moisture of the surface soil. Slope modifies the intensity of insolation by shifting the angle of incidence of the sun's rays. It also has some influence upon light, wind, and indirectly upon the distribution of snow. The depth of soil and water content vary almost directly with the gradient when other conditions are similar. As forest vegetation, however, is far less exacting than agricultural crops, land may be successfully used for forests that is far too steep for farm crops. Because of better drainage forest growth as a whole is better on land having a moderate slope than on areas that are nearly or quite flat.

Grebe's (1886) classification of forest areas in reference to gradient is as follows: gentle, 5 to 10°; medium, 11 to 20°; steep, 21 to 30°; very steep, 31 to 45°; and precipitous, over 45°.

It is recognized that gradients between 5 and 30° are best suited for forest growth. When the gradient is above 45° there is usually little or no forest growth.

On level situations, soil is deepest and roots are able to develop freely. As a rule, there is a maximum growth in individual trees. There are, however, certain disadvantages, which at first are not perfectly obvious. Frequently the soil is not well drained and tends toward swampiness; sometimes there is less favorable consistency of the soil; humus does not decompose as rapidly as on slopes, and in some places cold air settles and causes damaging frosts. On the whole, however, level situations are more favorable than any except moderate slopes.

Gentle slopes have soil of fair depth, and usually have a plentiful supply of moisture. Tolerant trees whose crowns overlap to some extent grow in very dense stands with a larger number of trees per acre than on level ground. Gentle slopes produce the highest yield per acre provided climatic conditions are favorable.

Medium slopes have moderately deep soil and usually a fair supply of soil moisture. They support dense stands and produce a high yield of timber under favorable climatic conditions.

Steep slopes usually have a shallow soil. Certain trees thrive upon them, especially those with shallow roots.

Very steep slopes have a thin soil usually with many rocks and boulders scattered on the surface and with more or less exposed rock in place. They are usually covered with short and stunted trees.

Precipitous slopes do not sustain a continuous forest, but rather scattered individuals and groups of trees, where enough soil has accumulated to sustain tree life.

In mountainous regions vegetation on the steeper slopes is exposed to heavy rainfall, sometimes causing washouts, floods, and landslides. On such slopes the snow cover melts earlier and often slides into and down the valleys in avalanches (Braun-Blanquet, 1932). Avalanches destroy forest growth and prevent its reestablishment on steep slopes. Steepness of slope may also affect forest succession and the development of both soil and vegetation climaxes through its influence upon the attainment of equilibrium in the slope.

4. EXPOSURE

The exposure of a particular site refers to its aspect with reference to the points of the compass. It is the direction of the slope of the land. The exposure of a slope determines the amount of sunlight received by a site. This, in turn, modifies the moisture content and the temperature of the soil and air. A poleward slope is considerably moister and cooler than one on the equator-side of a mountain.

Exposure influences forest growth chiefly through its effect upon temperature and soil water. It helps to determine the kind of vegetation present. Thus a slope exposed to the sun and wind often bears a different vegetation from one less exposed to either. Great differences may exist in temperature and atmospheric humidity on different exposures only short distances apart. Vegetation on the north-facing slope of a deep railroad cut is often quite unlike that on the south-facing slope, owing to the effect of exposure. The amount of heat absorbed by the soil on a given site depends largely upon how near to the vertical are the rays of the sun that strike it. In our latitude, the rays strike the soil much more obliquely on north-facing slopes than on south-facing slopes; hence the former receive much less heat than the latter where the rays are more nearly vertical. As greater heat increases evaporation from the soil, southern exposures are also much drier. The effect of exposure on heat is so pronounced that trees often are grown far south of their natural range on north-facing slopes and far north of their natural range on south-facing slopes. Trees are usually found at the northern extension of their ranges on south-facing or west-facing slopes. In mountain regions trees grow at altitudes lower than

their normal range on the cooler, northerly exposures and above their normal range on the more sunny and warmer southerly slopes. Because of the effect of exposure on soil water, forests are not infrequently entirely excluded from southern and western slopes; whereas northern and eastern slopes at the same elevation are well forested. This is particularly true of the mountain forests of the southwestern United States where there is low precipitation. The warmer and drier southerly exposures in dry regions are not favorable to forest vegetation.

To a considerable extent the effect of exposure is modified by latitude, its effect increasing with distance from the equator. It is also modified by the gradient or steepness of the slope and by the action of air currents. When the gradient is such that the sun's rays strike the soil vertically, the effect is greatest. The prevailing wind may be such that one slope may be much more subject to its action than another, irrespective of exposure. In such cases the modifying effect of exposure may be entirely overcome by the desiccating action of hot winds. In seeding and planting in dry mountain regions attention should be given to exposure, because regeneration often fails on southerly and westerly slopes where it is successful on northerly and easterly exposures. In artificial regeneration on our western mountains, except in regions of heavy precipitation, planting and seeding are most successful on north-facing slopes. In regions of moderate or scanty precipitation forest nurseries should be located on northerly slopes. The lower temperature will prevent early growth and lessen the danger from spring frosts; the danger from heaving of the soil and consequent injury to plants will be much less; and young seedlings will suffer less from drought.

The east slope has the early sun and is in danger of too rapid thawing after frost. The site is protected from southwest and west winds, and from the sun during the hottest part of the day. It is a favorable slope for tree growth and is frequently characterized by dense stands with good rate of growth and excellent quality of wood.

North slopes in the northern hemisphere are protected from the sun during most of the day, and in most localities protected also from winds. There is a maximum amount both of atmospheric and soil moisture. There is, therefore, usually an excellent growth of trees. In cold climates, however, sheltered north slopes are less favorable than warmer southern exposures.

A south slope is warm and relatively dry. Except when too dry, as in parts of the southwestern United States, humus disintegrates rapidly. The soil dries out quickly, the vegetation starts early, and is often

exposed to late frosts. Fires are more destructive than on north slopes. West slopes are also warm and dry.

The differences in insolation, soil temperature, and evaporation on north and south slopes largely account for differences in the vegetation on them (Gail, 1921; Bates, 1923, 1924; Shreve, 1924; Pearson, 1931). The contrast in forest vegetation between north and south slopes and between east and west slopes is particularly sharp in many of the higher mountains in the western United States.

5. SURFACE CONDITIONS

The surface of an area, especially of forest land, often shows irregularities such as outcropping rocks, animal burrowings, and depressions caused by uprooted trees, which retard runoff and cause a greater portion of rainfall to soak into the soil. These surface irregularities usually can best be described in terms of an even or uneven surface and by indicating the kind and amount of unevenness. In describing the surface conditions of forest land both the living and non-living soil covers are commonly included. They profoundly affect all the direct soil factors. They appreciably affect soil temperature by decreasing fluctuations in the surface layers. The non-living soil cover increases soil moisture by checking loss through evaporation. It appreciably affects aeration and influences soil composition through its effect on erosion.

6. Non-living Soil Cover

The direct effect of the non-living cover on the soil and the indirect effect upon vegetation depends upon its amount and its relative looseness. The looser it is, the more favorable its effect in absorbing water, retarding evaporation, increasing soil moisture, reducing radiation, and diminishing the extremes of temperature.

The two most important kinds of non-living soil cover are:

1. Snow.
2. Forest litter (fallen leaves, twigs, and dead herbage).

7. **Snow.** — Snow is an efficient protector of vegetation during the winter, as it shields the surface soil and the contained roots from excessive cold. In alpine regions and in arctic regions where the topography and wind currents are such that the snow covering is blown away, there is an entirely different vegetation from that in snow-clad depressions. The distribution of the covering of snow often determines the boundaries of plant communities. Snow drifts and deep snow patches, on

melting, deposit a fine fertile soil composed of organic and inorganic particles collected from the air by the falling and drifting snow. The importance of the snow blanket to forest growth and its value in many localities in making seeding and planting successful must be taken into account. In general, regions having a heavy fall of snow and at the same time adequate summer warmth to sustain growth produce heavy forests. In the forests of the Sierras of California a fall of 20 feet or more of snow occurs in a single winter. The summers are hot and dry. This heavy blanket of snow prevents the soil from freezing and drying out in winter. When the snow melts in the spring the soil becomes thoroughly saturated, for the snow melts slowly. In regions of scanty snowfall and extreme cold, few trees are able to persist because of the severe freezing and consequent drying out of the soil. Under similar amounts of precipitation, regions like California with a heavy winter precipitation, chiefly snow, will sustain forests; whereas regions like Dakota and Nebraska with a scanty winter precipitation but heavy summer precipitation, are chiefly prairie. In the latter, forest plantations suffer severely from winter killing and can be established only by planting the most resistant species with special care and attention. Snow influences plant form by its weight, often causing trees to assume prostrate forms. In regions of extreme cold the parts exposed above the snow may regularly freeze back, causing trees to become shrub-like, or to develop low, umbrella-like crowns.

Deep snow acts as a defense against loss of moisture by transpiration. Thus many tender shrubs and trees in their juvenile stage are able to survive the winter because of snow protection, the parts buried beneath the snow not losing moisture when the transpiration current can not be supplied by the roots in the frozen soil. On sites of great snow accumulations the snow is very important as a water reservoir, the depth of the winter snow determining the amount and luxuriance of vegetation the following growing season. A heavy covering of snow shortens the growing season because plants are prevented from becoming active as early in the spring as on snowless sites.

Deep snow compacted by wind and storms often has an injurious effect on forest vegetation, particularly when it lingers late in spring, because it may cause suffocation by restricting the supply of air and by favoring the development of snow-smothering fungi (Korstian, 1923). On the other hand, the snow, in protecting the soil from the alternate heat of the day and cold of the night, prevents change in soil volume and the consequent uprooting of small plants and the rupturing of the surface roots of larger ones.

8. Forest litter. — By litter is meant the undecomposed organic matter lying on top of the layer of humus. It is composed of fallen leaves, branches, twigs, dried herbage, and other débris lying in a forest. It is continually being replenished from vegetation and is continually being consumed by decomposition in the formation of humus. It has the same mechanical effect as snow in keeping the soil more moist, and more uniform in temperature. As the layer of litter is present in the growing season as well as in the winter, it has a well-marked influence on the kind and character of living ground cover such as moss, herbs, and tree seedlings, which it tends to suppress.

9. Living Soil Cover

Every kind of covering over the soil, formed by living vegetation, affects the soil and through it the trees. The denser, taller, and longer lived the vegetation is, the greater is its effect on the soil.

Both the physical and chemical relations of soil are affected by the living ground cover. Thus temperature of the soil is modified, the cover acting as a screen against the sun's rays; fluctuations in temperature are less; the amount of water in the soil is influenced; the soil is less compact; light reaching the soil is less; action of the wind is decreased; and the air underneath the vegetation is cooler and moister. Under more than 0.7 density in the forest canopy the lower ground cover has a diminished effect on the quality of the soil. Under abuse and a lower density, however, the soil may become covered with vegetation which may reduce its quality.

Ordinarily, scattered grasses in a forest have no significance. Extensive clearings, however, may be covered with a dense growth of grass. The principal effect of grass is seen in its relation to the reproduction of forest trees. Tree seedlings compete under difficulties with grass. Ferns are of little importance in forestry, except in places where they impede reproduction and occasionally where they tend to form raw humus.

Scattered shrubs and young tree seedlings in a forest have very little effect on the soil. More often than not they help shade the soil and are beneficial rather than otherwise. Poor forest management sometimes results in an almost complete covering of the soil with blueberry bushes and other ericaceous shrubs. These tend to form a compact network of roots near the surface of the soil, which has an injurious effect in withdrawing moisture and in preventing reproduction. The living soil cover affects the chemical relations of the soil only by its removal in whole or in part.

CHAPTER IX

BIOTIC FACTORS

Aside from the physical (climatic, edaphic, and physiographic) factors already discussed, the distribution, form, and structure of forest vegetation is much influenced by the community life of organisms, both plant and animal. The effect of community life is imprinted on forest vegetation and also on the site itself. The complex relationships, both mutual and antagonistic, between plants and between plants and animals profoundly affect forest vegetation as a whole. The biotic factors are not, however, amenable to exact methods of measurement as are the physical factors. The main relationships involved in the biotic factors are as follows:

1. Reaction for growing space as expressed in competition.
2. Interrelationships between plants.
3. Interrelationships between plants and animals, particularly the effect of animals.
4. Interference by man.

It should be clearly appreciated that these biotic factors do not form part of the physical complex of the site but express influences or reactions exerted upon the site.

1. COMPETITION

Whenever trees grow close enough together to form stands, competition occurs; that is, there is a struggle between individuals for their existence. In both fully stocked and overstocked naturally developed stands, intense competition occurs for light and growing space above the forest floor and for growing space, soil moisture, and nutrients below (Korstian and Coile, 1938). Competition results in the overtopping, suppressing, and crowding out of the weaker trees by more vigorous and more aggressive individuals, and this results in a natural " survival of the fittest." A tremendous struggle occurs in forests growing in moist to wet situations as they develop from very dense stands of reproduction to mature forests. For example, reproduction of southern white cedar, which is strictly a swamp tree and which commonly forms extremely dense stands when young, has been found to have up to 52 seedlings per square foot or over $2\frac{1}{4}$ million to the acre. Only 200 to 300 trees per acre may reach maturity on the better-quality sites (Korstian and Brush, 1931).

The composition of mixed forests is largely determined by the relative aggressiveness of dominant species. The aggressiveness of a species depends upon the ease and rapidity of its reproduction, its rates of spread, growth, and expression of dominance, and its light, moisture, and soil requirements. In short, stand composition is determined largely by the relative capacity of various species to occupy a site permanently in spite of the struggle with their competitors for existence. The expression of dominance is a natural sequence of early competition between plants; and the earlier dominance is expressed and maintained by a species the greater the probability of its survival, other factors being comparable (Deen, 1933).

It is a common observation that over many parts of the earth certain species are excluded because of the intense struggle among plants for growing space. Thus certain species are excluded from a given site, not because the physical factors are unfavorable, but because of disadvantageous reaction of other plants which involves competition for light, water, and nutrients. Since the time of Darwin attention has been directed toward advantageous and disadvantageous reactions among plants as factors affecting the distribution of species and the forming of plant communities. The importance of this is shown in the fact that a given site may sustain an arboretum of several hundred species from widely separated parts of the world. Various species are maintained so long as competition is withheld. If, however, they are left to themselves, only a few survive. Indigenous species form the larger number of those that survive in competition for growing space. As a rule most tree species are not especially exacting in regard to soils so long as they have no competitors. Within the natural range of a species, however, its local occurrence is determined largely by competition. The post oak in Connecticut grows on dry, poor, shallow soils, not because it grows best on such soils but because it is excluded from the deeper and more fertile soils through competition with other hardwoods.

As pointed out by Warming (1909) the competition between beech and oak or between other economically important forest trees is not completely comprehended. Obviously there are many factors which determine survival when two or more species grow in mixtures of which growing space and the question of nutrition are only a part. Individuals in a community of living plants have their lives so interwoven that a change in any one of many factors may so change other factors as to bring in its wake far-reaching changes in vegetation. Although these changes are referred to as the result of competition, it is as yet impossible to analyze the components which cause the changes.

2. INTERRELATIONSHIPS BETWEEN PLANTS

The interrelationships between forest plants are numerous and are exhibited in varying degrees of dependence. As emphasized by Warming (1909) interrelationship is shown in all degrees of bondage from parasitism to the interdependence of plant communities. This is of far-reaching importance in forestry, and particularly so during invasions by parasites, as exemplified in the widespread destruction of the chestnut by blight (*Endothia parasitica*). Parasitism, in which forest trees are the hosts for multitudes of parasites, is in evidence in every forest. In this case one species provides the other with nutriment at the expense of its own living tissues. Most dependent of all are those plant parasites, like the white pine blister rust and the chestnut blight, which are incapable of utilizing inorganic nutrients and can live only upon a definite species or group of closely related ones. Less dependent are the mistletoes which can live upon several or many kinds of hosts, all of which may not be confined to the same family and which, although rooting in the host and obtaining the mineral nutrients from it, are capable of photosynthesis (Bray, 1910; Weir, 1916; Korstian and Long, 1922). Most species of plant parasites can exist only as parasites; some, however, are less exacting and can live also as saprophytes.

The relationship that exists between the plant parasite and the host is always a hostile one. The parasite is a robber, for it deprives the host of energy without compensation. Not uncommonly the host is killed by the parasite and sometimes a species is practically exterminated for considerable periods, over extensive areas. This antagonism between the host and the parasite has a very important bearing upon the composition of the forest community as is seen in the present reaction between the chestnut and the blight fungus in southern New England which has changed the character of the forest vegetation in the entire region (Korstian and Stickel, 1927).

Forests composed of but a single species suffer most from parasitism, for parasites spread much more rapidly through a pure stand than through a mixed assemblage of trees. Parasitism alone may in some instances cause one species to be replaced by others.

In contrast to parasitism we sometimes find in the forest a sort of mutual reciprocity between plants. Neither plant is seriously injured by the relationship existing between them but usually both are benefited. This kind of relationship is illustrated in the mycorrhizae on the roots of pines and many other trees and in the tubercles on the roots of black locust and other leguminous plants.

Mycorrhizae represent a mutualism in which the roots of trees and of other highly organized plants are intimately associated with fungal hyphae, either ectotrophically or endotrophically. Ectotrophic mycorrhizae form a sheet enveloping the slender roots and root tips. Endotrophic mycorrhizae live in the cells of the root cortex. It has been demonstrated that, in some instances at least, there is an interchange of nutritive materials between the root and the fungus. It is believed by some that the mycorrhizal fungus absorbs the nutrients with the soil water and transfers them to the roots, but to what extent one plant aids the other is by no means definitely settled. How much the presence or absence of mycorrhizal fungi in the soil is responsible for the presence or absence of various species of trees on particular sites is also uncertain. There is convincing evidence that mycorrhizae aid trees in obtaining nitrogen from humus which contains little or no nitrates.

The relationship which exists between the bacteria in the nitrogen tubercles on leguminous plants and the plants themselves is somewhat similar to that of endotrophic mycorrhizae. Here, as illustrated in the roots of black locust, the small tubercles are occupied by bacteria which assimilate the free nitrogen of the air and make it available for the trees.

Epiphytes do not derive food from the living tissues of other plants but at most only from their dead parts. Their relationship to other plants is that of finding mechanical support upon them and thus access to the light. When in great abundance, they may injure the supporting tree by causing excessive humidity and diminishing respiration and by cutting off the air and light, as is sometimes the case with *Tillandsia* on live oak and other species in the southern United States. Epiphytes, with the exception of those which occur in very humid forests, have special adaptations to overcome injury from drought, as their water supply is wholly obtained through absorption from the atmosphere.

As saprophytes obtain their carbon nutrients from the dead parts of other plants, their interrelations with living trees are of an entirely different nature from that represented by parasitism. Some saprophytes appear to live on the dead tissues of particular species, hence are associated with those species. Most saprophytes, however, are associated with a great variety of species, often of widely different genera, for example, most of the fleshy fungi so characteristic of forest communities.

Lianas (climbing woody vines) are associated with other plants in that they depend upon them for mechanical support. Their origin is

due to the community life of plants. Their presence in a forest gives it characteristic physiognomy. They exhibit diverse adaptations to facilitate mechanical support on other species. Certain species like poison ivy are root climbers; others like bittersweet are twiners. A large variety of other lianas climb by means of irritable organs known as tendrils. The latter is illustrated in the grape and Virigina creeper. Although the liana type is a result of the congregating of plants into communities, inanimate supports serve them quite as well as living ones.

The preceding paragraphs dealing with the relationships between plants relate to the bonds that link one plant with another; there is, however, an entirely different kind of interdependent relationship existing in forest communities. In each recognizable community are a number of growth forms. These combine to form a single aggregate which has a more or less distinct and constant appearance. *Commensalism* is the term usually employed to denote the relationship between growth forms which in a single forest community share with one another the space and food materials in the soil and atmosphere and are therefore capable of existing together. A forest community may be composed of like or unlike commensals. A pure stand of beech or white pine is a good example of like commensals. Such a tree community is composed of a single species in which all its members make like demands on the site. As the trees develop and make greater demands for growing space, individuals in unfavorable spots and weaklings are eliminated. This competition between like commensals takes place in every closed stand. In open stands, where competition is absent, like commensals form the plant community when the site factors are unfavorable for the introduction and development of other growth forms.

Almost always a great variety of species and growth forms grow side by side in a forest community. These unlike commensals, although living together, make unlike demands on the site, for when one species occupies a given area as completely as the soil will permit, others making different demands on the soil find space between the individuals of the former. In every forest community of unlike commensals there are numerous species which differ widely in the demands they make for light and nutrients. The wider the difference the less the competition between them. In almost every forest community, however, there is a limited number of species and growth forms which are most potent and which dominate and hold sway over the site. The term complementary association has been used to denote tree species which live together

in complete harmony because they draw upon different depths of the soil and have different light requirements. The opposite extreme is provided in competitive association where the different species draw upon the same depths of soil and have the same light requirements.

3. Importance of Plant Parasites

Foresters are concerned not only with the volume of timber that a given area of forest land is capable of producing but also with that part of the yield which external agents may destroy or render useless. Although, as pointed out by Meinecke (1916), we do not know what this loss is and have not resolved it into its several components and studied each in turn, we do know that parasitic plants, next to man, fire, and possibly insects, are the greatest biotic agents in reducing production and in changing the form and structure of forest communities.

Parasitic plants and their effect on the host are comprehensively treated by Hartig (1894), Rankin (1918), Hubert (1931), Boyce (1938), Baxter (1943), and others in numerous manuals, bulletins, and technical journals. They cause enormous losses in virgin and other forests which are largely depended upon for lumber. Foresters have been slow to adopt sanitation methods by which these losses can be reduced.

In general, plant parasites which inhabit forest communities may attack and destroy the leaves, branches, boles, roots, and even the flowers and fruits of forest trees. Sometimes the young seedlings are destroyed by damping-off parasites (Hartley, 1921), not infrequently soon after the seeds germinate and even before the seedlings appear above the surface of the soil. The losses are greatest soon after the young plants show above ground, and they are caused by various fungi which inhabit the soil. They are chiefly species of *Pythium*, *Rhizoctonia* ("Corticium type"), *Fusarium*, *Corticium*, and possibly *Phytophthora*, which usually attack the root or the hypocotyl after the seedling has appeared above the soil and while the stem depends upon turgor to maintain itself in erect position. Damping-off may, however, occur by root infection even after the stems have started to become woody. Normal types of damping-off are recognized by the young plants' withering at the surface of the soil and losing their erect position. They die in a few days after infection takes place. As the seedlings of some tree species are much more susceptible to infection than others, damping-off is one of the factors in shaping the composition of mixed stands.

Variously colored spots on the foliage of trees caused by parasitic fungi are the most common diseases of some forest communities. There

is scarcely a tree that does not support one or more of these leaf parasites. All these leaf-spot diseases are characterized by dead areas of variously colored tissue occupying a greater or less proportion of the entire area of the leaf. In severe infection, the tree becomes more or less defoliated. Although they seldom, if ever, kill the host, they reduce the area of functioning leaf surface and are often responsible for a rapid falling off in yield. A large number of these parasites, the most common of which are known as rusts and mildews, infect every forest; but direct methods of control are usually impractical.

Parasitic fungi infecting the living tissues of the bark and wood, particularly the cambium, are much more destructive than diseases confined to the leaves. Such diseases are often difficult to locate. Although they may gain access through the stomata in the epidermis of the leaves and through young branches before the cork tissue develops, later they gain access only through openings in the bark caused by insects, fire, frost, and other external agents. Parasitic fungi seldom cause lasting damage by destroying leaves as new leaves replace the old. In bark and wood parasites, however, the disease is usually progressive and almost invariably the tree in time is killed. The infection may be active for months or even for years in the tissues of a tree without there being any external evidence of the presence of a parasite, as in blister rust on white pine. In time, however, fruiting bodies appear on the surface which reveal the presence of a parasite. Many of these wood and bark parasites, because of their power to destroy both young and old timber and also because a given parasite usually infects but a single tree species, have far-reaching importance in determining the character of forest communities and the composition of stands.

In the past 35 years, the chestnut blight (*Endothia parasitica*) has practically exterminated the chestnut as a commercial species over its entire range. During the past 25 years, the white pine blister rust (*Cronartium ribicola*) has become a serious menace to white pine in many localities in the northeastern United States.

Wood-rotting fungi invade the roots, stems, and branches after they have lost their protoplasm and have become essentially dead tissue. It has been estimated that, were it possible to eliminate the factor of decay in all standing timber, the yield from mature and virgin forests would be increased by at least one-fifth. The fungi which destroy wood while still standing, many of which advance into and kill living tissue in the sapwood and bark, are mostly of one type and belong to the order *Hymeniales*. As a rule, the infection enters through wounds in the bark. Normally a tree is protected from invasion by its bark,

but where the bark is injured, exposing sapwood or heartwood, infection is likely to occur. The wood is gradually destroyed and the tree becomes hollow, and worthless for economic use. Species which attack sapwood spread their mycelia in all directions soon after infection and cause large areas of dead tissue to appear on the surface of a tree. In time, but usually after damage has been done, the presence of wood-rotting fungi is revealed by the appearance of fruiting bodies at or near the base of a stump or along the bole of a standing tree. These bodies continue to appear on dead timber long after it has fallen to the ground and not infrequently after it has been manufactured, if used on the ground where exposed to considerable moisture.

Although wood-rotting fungi greatly affect the yield of timber and occasion enormous losses in American forests, they are more completely amenable to control than diseases caused by most other classes of parasitic plants. Control measures, as emphasized by Meinecke (1916), center in forest management and silvicultural measures to keep the stand in thrifty condition, and in cutting infected trees and utilizing the timber before it becomes overmature or begins to decline. The disposal of infected slash so as to reduce the production of fruiting bodies reduces infection in succeeding crops.

4. EFFECTS OF ANIMALS

The presence of animal life in a forest is often of great importance in the practice of forestry. The interrelationships between forest plants and animals are many and variable. All degrees of bondage or interdependence exist, from parasitism to mutual benefit or even mutual necessity. The interdependence between animals and plants is usually more obligatory and inevitable than that between plants alone or between animals alone (Taylor, 1935). These interrelations are shown in the fact that the distribution of certain trees and of certain forms of animal life coincide, because of reciprocal relations, one to another. Although most trees of temperate regions are wind pollinated, localities rich in insect life sustain a vegetation in which the flowers are often showy and adjusted for insect pollination. Protective means against animal life, reciprocal adjustments between trees and insects, structural developments that aid in seed dispersal by animal life are only a few of the numerous ways that a plant community is adjusted to the animal life therein.

In spite of the significant interdependence between forest animals and plants, foresters most commonly consider animals from the standpoint of their effects upon forests. The varied forms of animal life that

directly or indirectly affect forest vegetation are exceedingly numerous and of vast importance in determining the character of forest communities. Some forms are of constructive and others of destructive significance in forests. Although many animals are of considerable importance in a forest and their presence should be encouraged, others, as illustrated by many rodents, though of constructive usefulness in distributing seed, are significantly destructive in eating seed and in injuring or destroying young plants. Others are usually wholly destructive, as most mammals and many insects. They feed upon foliage or fruit and return nothing in compensation for the loss incurred. The initial establishment of natural reproduction of certain forest trees may be materially affected, if not actually precluded, by animals destroying the seed (Korstian, 1927; Haig, 1936). One of the special functions of forest protection is to guard against invasions by destructive insects and to control damage by various animals, both domesticated and wild.

Many terrestrial animals are wholly dependent upon plants, which constitute their primary source of food (Pearse, 1939; Shelford, 1929). Wherever forest plants, seeds, or fruits are used for food by animals or mankind very significant coactions commonly occur. Outstanding food coactions, strikingly illustrating the bad effect of uncontrolled mammal life in forests and its influence in modifying forest communities, are witnessed in overgrazing by domestic animals and selective browsing by deer. In these examples the logical assumption is that the coaction is wholly beneficial to the animals and injurious to the forest vegetation. The extension of grazing range at the expense of forests in the western United States is favored in certain localities where animals feed upon bark, buds, leaves, twigs, branches, stems, and roots of forest trees (Taylor, 1936).

5. Domestic Grazing Animals

The grazing of domestic animals on forested areas is of common occurrence in the United States. The vast economic interests involved and the urge to utilize fully wild forage of all kinds tend toward overgrazing forests in many parts of the country, thus checking natural reproduction and decreasing growth. Wasteful and uneconomic overgrazing, which destroys reproduction and, if persisted in, will destroy forests, reacts upon forage plants themselves and reduces the carrying capacity of a range. The bad effects from overgrazing are usually more pronounced in hardwood than in coniferous forests. The prefer-

ence of most animal life for hardwood browse tends to favor coniferous species in mixed stands. Overgrazing in general reacts on soil, on reproduction, and to some extent on forest fires. The soil is rendered compact and more or less impermeable to air and water, making it more difficult for reproduction to start and become established. The destruction of herbaceous vegetation on the forest floor through grazing, particularly on slopes, increases erosion. Furthermore, animals tend to form and follow trails which become important centers for erosive action. Not only does overgrazing reduce reproduction through its effect on the soil, but it greatly reduces survival after germination takes place. Many seedlings are killed, others are so trampled or otherwise injured that they do not recover. Generally, grazing that will materially injure forest reproduction is overgrazing from the standpoint of forage production and utilization and should be eliminated. Seeds are eaten and young plants rooted up and destroyed by hogs. The grazing of hogs in longleaf pine forests almost completely eliminates natural reproduction of that species in parts of the South (Chapman, 1926; Wahlenberg, 1946).

Even after the crowns grow up beyond the reach of goats the thin bark of seedlings and saplings is gnawed and peeled, thus killing or severely injuring it. In most instances, however, when the trees once elevate their crowns above the reach of domestic animals they are free from further direct injury. Indirect injury, however, may continue to take place because of the effect of the stock on the litter and in compacting the soil. Overgrazing, by reducing the vegetation on the forest floor and the amount of litter, greatly reduces the fire hazard. In most localities, however, its good effects in this respect are overbalanced by the generally accepted fallacy that surface fires improve the grazing. Leopold (1924) states that in some places in the southwestern United States overgrazing by the elimination of grass greatly reduces competition between grass and trees and has resulted in a succession from grass to forest. However, studies in northern Arizona, extending over a series of years, have shown the injurious effects of sheep grazing on the reproduction of ponderosa pine (Hill, 1917; Pearson, 1923). Comparable damage to reproduction of the same species has been observed in central Idaho (Sparhawk, 1918). There is uniform failure of natural reproduction of this species in northern Arizona, except where seedlings start in large numbers in advance of cuttings. This failure is due not to improper methods of cutting or to unusually adverse climatic conditions but primarily to excessive sheep and goat grazing. Reproduction can be obtained with reasonable

certainty by present methods of cutting, provided damage by grazing is eliminated (Pearson, 1923).

Sheep are responsible for severe damage to aspen reproduction in the Intermountain and Rocky Mountain regions (Sampson, 1919). Cattle also cause some injury to aspen, but the extent of damage is usually not severe, except where forest ranges are overgrazed or where animals congregate repeatedly, as around watering places (Korstian, 1921).

Serious damage to a forest from grazing can be averted by closing cut-over areas to sheep grazing until the reproduction is above the height at which injury occurs and by properly regulating the grazing of all livestock at other times.

6. Deer and Elk

In general, deer and elk cause the same type of injury as that caused by domestic animals. They are especially damaging to small reproduction and when abundant they may, through selective browsing, materially shape the composition of the stand. However, the number of elk is so small that, with the possible exception of the Jackson Hole area in Wyoming, their damage is not serious. The number of deer is also commonly too small to cause serious injury to forests except on occasional heavily overstocked areas as in the Kaibab and Pisgah National Forests and in portions of Pennsylvania and Michigan where they have increased greatly within recent years. Studies made in an understory of red and white pines growing under gray birch near Keene, New Hampshire, showed 84 percent of the leaders and important side branches of the white pine eaten off in a single winter, whereas the red pine was untouched.

Under present economic conditions, the regulation of the kill during the open hunting season is probably the most practicable method of restricting the amount of injury by deer whenever that injury becomes serious. Wherever cleanings are being made in plantations or in young stands of reproduction, lopped branches or small trees may be laid over trees to protect them from deer browsing (Clepper, 1931). In Germany young spruce trees removed in cleanings have been stuck upside down in the ground to protect small larch seedlings and saplings from deer injury.

7. Beaver

Beaver, although relatively scarce, often change the physiographic characteristics of the site and completely change soil moisture condi-

tions by erecting dams at the outlets of lakes and along streams. They not only cause the death of timber by flooding, but they change the composition of stands by the selective felling of trees, often of merchantable size, in the vicinity of their dams and ponds.

Beaver prefer certain tree species, particularly aspens, and will go considerable distances for their favorite species if they are not available nearby (Warren, 1926; Johnson, 1927). Beaver may fell or girdle all trees of the preferred species adjacent to their ponds. However, their greatest damage often results from the destruction of entire stands immediately upstream from their dams by raising the water level of the ponds and streams sufficiently to submerge the root systems of the standing trees and thus kill them.

8. Rabbits

Rabbits, particularly snowshoe rabbits, are periodically so abundant and destructive as to prevent reproduction locally. Seedlings and small trees are subject to most of the injury by having buds, small branches, and stems cut off and the bark gnawed, which frequently results in the death of trees. Rapidly growing shoots of seedlings, recently planted or freed by cleanings, are usually preferred by rabbits to more slowly growing trees. Rabbit damage to trees is more serious in regions where heavy snowfalls cover up other readily available sources of food (Baker, Korstian, and Fetherolf, 1921).

9. Squirrels

Several species of squirrels may often have an important bearing upon the establishment of reproduction and the growth of trees. They eat the seeds and fruits and cut off young twigs and buds of many tree species (Hosley, 1928; Hatt, 1929). They may devour, destroy, or cache essentially all the seed produced by a species. Sometimes squirrels and other small rodents bury, in the litter and soil, tree seed which later germinates and contributes additional reproduction (Korstian and Baker, 1922). Besides the seed of some conifers, squirrels are known to distribute the seed of oak, hickory, and chestnut.

Girdling of jack pine by red squirrels in Minnesota and ponderosa pine in the Black Hills has been reported (Pike, 1934). In the Black Hills trees 4 to 7 inches in diameter have been completely girdled at points 10 to 20 feet from the top, leaving spike-topped trees.

10. Porcupines

By far the most serious damage by porcupines is their gnawing of the bark from standing live trees. During the late summer, autumn, and winter months, in their efforts to get at the inner bark, they often partially or completely girdle the main stems, with the result that trees are weakened, bushy topped, or spike topped (Gabrielson and Horn, 1930; Taylor, 1935). Injury may be inflicted on any part of the bole or on the branches as a porcupine climbs a tree, so that, whenever barking results in girdling, the portion of a tree above the wound dies. Where porcupines are abundant many seedlings are completely consumed or ruined and larger trees are frequently injured seriously enough to cause their death. In areas of heavy infestation, 10 to 100 percent of the young growth in ponderosa pine stands may be thus damaged. In and near the Harvard Forest, in central Massachusetts, porcupines have seriously damaged European larch and Scotch pine in plantations and native hemlock, particularly by barking and girdling the trees (Hatt, 1930).

11. Mice

The seeds of many forest trees are eaten by mice. When food is scarce during the winter, mice gnaw the bark from seedlings and young trees, often working under the snow, either above or below ground, and frequently girdling and killing the trees. Mice may increase periodically to such extent as to do serious damage to most of the trees on restricted areas (Hatt, 1930). However, through preference for certain species girdling by mice may materially change the composition of mixed stands. By maintaining the proper balance of predatory animals, such as, hawks, owls, snakes, and carnivorous mammals, an excessive increase in number of mice can be prevented. Some mice are actually beneficial to a forest by feeding on pupae of the larch sawfly and thus preventing these insects from becoming epidemic (Graham, 1928).

12. Birds

The beneficial influence of birds greatly outweighs their injurious effects upon forests (McAtee, 1926). They are important agents in the natural dissemination of seed of tree species having fleshy fruits, such as red cedar, black cherry, and black gum. Birds are of great value in reducing damage from insects and smaller rodent pests by

feeding upon them (Adams, 1923; McAtee, 1926). In the natural reforestation of both burned and cut-over lands birds may have an important rôle. Birds consume a large amount of forest-tree seed, bite off the tops of young seedlings, and peck holes in trees. Blackbirds are reported to have seriously injured a pine stand by roosting in it repeatedly, thus adding sufficient droppings to the soil to increase its nitrate nitrogen content to injurious proportions (Stewart, 1933). However, on the whole, birds, because of their recreational and aesthetic values and generally beneficial influence, should be protected and encouraged to increase in forests.

13. Insects

The pollination of many tree species, such as black cherry, black locust, and basswood, occurs through the agency of insects, thus making seed production possible. However, invasions of forests by destructive insects are by far the most important interrelations between the forest and animal life having both ecological and economic significance. Some species destroy seed, others buds, others foliage, and others weaken trees by sucking sap from the leaves. Some species cause galls and other deformities, others bore into bark, wood, or pith of the shoots or roots and in time cause the death of trees or render the wood of little economic value. An epidemic of tree-destroying insects may, and often does, kill a large part of a standing timber crop in a relatively few years, as illustrated in the invasion of the spruce and balsam fir forests by the spruce bud worm (*Archips fumiferana*) and the ponderosa pine forests by bark beetles (Graham, 1929; Doane, Van Dyke, Chamberlain, and Burke, 1936). The killing of a considerable part of a stand of timber at one time greatly increases the amount of inflammable material and hence the fire hazard. Fungous diseases are likely to follow insect infestations, the fungi gaining access through openings made by the insects.

14. INTERFERENCE BY MAN

Of all the factors causing or contributing to deforestation or even tending to disturb natural conditions in forests, man has been the most powerful and persistent. Mankind has been primarily interested in forests only insofar as they could be made to satisfy human needs. In satisfying the many diverse needs for various products of forests, the manifold activities of the human race have profoundly modified

forest vegetation. In fact man has been at work changing his environment for the last 2,000 years, or ever since members of the human race became numerous enough to have much effect on natural environments (Marsh, 1882; Taylor, 1935). Obviously the original balance of nature has been completely overthrown by man in his conquest of forests through such activities as clearing of forested land for agriculture, unregulated cutting of timber in lumbering operations, grazing of livestock on forest areas, burning of forest and range lands, depletion of game and predatory animals allowing an unnatural increase in the rodent population, drainage, elimination of native plants, and introduction of plants and animals, some of which have become pests. Thus man has altered the condition and economic importance of natural forest areas. The old biological balance existent prior to man's interference with nature is gone forever, but in its stead new balances are constantly being reached. Man's modifications of nature should be such as to make new balances beneficial rather than harmful to the greatest number of people. The interrelationships involved in attaining a balance of nature are important features of all organisms and their environments, and this is especially true when man is considered in relation to forests.

The reciprocal relations between forests and mankind are many. Although forests affect the human race, the effect of man on forests is almost everywhere far greater and more far-reaching. Man has brought about pronounced changes in forests. In most regions formerly forested, man has modified or destroyed forests in order to use their products for commercial undertakings or to use the land for cultural purposes. A large percentage of the forest associations at present inhabiting the earth are therefore cultural.

In the more densely populated regions man has changed natural plant communities to cultural communities and brought about types of vegetation widely different from those resulting from other causes. Through his activities he has destroyed the natural plant communities, and by cultivation he has kept them from being replaced in kind. Through lumbering and uncontrolled forest fires, man has destroyed the vegetation on tillable and non-tillable lands alike until soil conditions have been so radically changed that replacement in kind is no longer possible within short periods of time.

The following relate to the more conspicuous reactions of man on forests whereby forest communities disappear or become more or less radically changed.

15. Agriculture

For centuries, because of the progressive increase in populations and the need for food crops in increasing quantity, natural forest communities have been replaced by agricultural crops. Countries like England, where the land was once almost completely in forests, have carried replacement so far that but few forests remain. Even in the eastern United States all the better land formerly covered with forest growth is now under cultivation. It is to be noted, however, that wherever tillage has been abandoned on areas originally covered with timber, the land slowly reverts to forest.

16. Lumbering

Lumbering carried beyond the exploitation of the timber on land required for agriculture is not of the same nature as the conversion of forest areas to wheat, corn, or cotton land, an essential economic need in every civilized country. It is devastation when a forest community is swept away without provision for replacement by either agricultural or forest crops. Without conscious care a forest is slow and uncertain in replacement in kind, and when soil conditions become changed, as is often the case on non-agricultural land, favorable conditions for forest growth are destroyed, and the soil must be built up through successive generations of plants before acceptable forest renewal is possible.

Such destruction, followed by devastating forest fires, has been in the past and is yet in the United States the greatest single factor in modifying forest communities and in changing the productivity of forest land. The grave danger to continuous forest growth from past methods of timber exploitation is not so much from the destruction of existing vegetation as from adverse reactions on the soil. These can be overcome only by conscious care and the employment of forestry methods in lumbering operations that lead to certain replacement in kind or with better species and that will produce full timber crops.

17. Introduction of Plants and Animals

The influences of man on natural forest communities brought about by the introduction of plants and animals are apparent in every civilized country. The present vegetation is so much the direct or indirect result of man's influence that there are few places where he has not in one way or another changed it from the original natural cover. He is constantly bringing in exotic plants and animals which compete

with indigenous species. The old-world mulberry and bird cherry are common in forest communities in New England and plants of old world origin are establishing themselves in competition with native species. Such introductions are not only modifying the economic status of our natural forest communities but are likely to cause changes which will modify and help control ecological structure.

18. Introduction of Pests

The disastrous reaction of biotic factors on natural forest communities is nowhere more in evidence than in regions infested by animal and plant pests introduced either directly or indirectly by man. The gypsy moth introduced into New England in 1868, through its characteristic mode of selective feeding, is gradually changing hardwood stands into coniferous stands (Clement and Munro, 1917). Species of *Opuntia* from America, introduced into South Africa and Australia, have become dominant over large areas and have forced the indigenous vegetation to occupy a subordinate position in the plant community. Weeds from Europe and elsewhere compete with our native vegetation and with cultivated crops. The most striking example of an introduced pest which has become epidemic is probably that of the chestnut blight (*Endothia parasitica*). Introduced from the Orient prior to 1900, it has greatly changed the composition of many of the hardwood forests of the eastern United States through widespread destruction of the chestnut (Korstian and Stickel, 1927).

19. Fire

Forest fires, largely caused by man, change natural forest conditions in all regions inhabited by him. Fire not only partly or completely destroys living forest vegetation but consumes the dead vegetation in various stages of decay and profoundly affects the forest soil through destruction of the litter. As soon as the soil has been made bare by fire it is reoccupied by invading plants of one kind or another. A new plant community arises in the ashes of the old. Trees and other forest plants enter and in time a forest again occupies the area. Usually, however, the new community is not like the old, largely owing to changed soil conditions. By repeated forest fires a forest community of economic species may be changed to forest weeds, scrub, or even to herbaceous growth. Because of differences in the resisting power of tree species, fire is an important factor in determining the composition of stands. On the whole, coniferous species suffer greater injury than hardwoods. Shallow-rooted species are less resistant than deep-rooted

species because of nearness of the roots to the burning litter. Old timber, which has thicker bark, is more resistant than young growth. Although fire under control may be a constructive agent and beneficial in forestry practice, uncontrolled fire is always harmful. It not only causes changes in forest communities but great economic losses in timber production. Economic losses from uncontrolled forest fires arise from the destruction of commercial timber and reproduction, the deterioration of forest soil, and the damage to water conservation. As many as 40,000 uncontrolled forest fires occur yearly in the United States which burn over from 6 to 7 million acres.

A detailed study of the rôle of fire in the pine forests of the California Sierra showed that, although fires in natural stands are mostly confined to the surface and are not catastrophic in nature, the damage they do has been minimized or ignored (Show and Kotok, 1924). This damage, however, though gradual and without display, is very great and is aptly termed attrition. Surface fires, though a single one is light in itself, when repeated at intervals, gradually cause the conversion of stands of tolerant species to less tolerant species and the progressive increase of shrubs, until there is an end of the forest altogether and a complete dominance of shrubs.

As second growth and other immature stands are much denser, fires in them are as a rule of the crown type. A single fire is a catastrophe, which may devastate an area, after which it is occupied by shrubs. Brush fields thus tend to perpetuate themselves because later fires are also of the crown type. The shrubs reproduce by sprouting, but the young trees that start are killed outright.

The recent destruction of a forest by fire and its effect upon the composition and character of the succeeding stand are generally apparent. The more gradual and indirect consequences of surface fires, however, which result in heat-killed trees, fire-scarring, and the impoverishment of the soil are much less apparent. They afford conditions favorable for fungous and insect epidemics and prepare the way for more severe fires in the future.

Although man is the chief factor in the initiation of forest fires, he is also the chief factor in their control. Forest fires are dependent upon available fuel supply. The presence of this material does not become a hazard, however, until it reaches a certain degree of dryness, which depends upon weather conditions. By watching weather conditions, particularly the relative humidity of the air, with which the moisture conditions of the litter are correlated, the degree of hazard can be predicted and the necessary precautions taken to prevent many fires from starting and to control promptly all fires which do start.

CHAPTER X

INTERACTION OF SITE FACTORS

A forest environment is in reality a complex in which a given factor not only acts upon the habitat and upon the other site factors but also is, in turn, acted upon by them. The effects of changes in site factors are reflected by functional responses, by differences in growth, and by changes in form and structure of the plants. Site factors fall naturally into two groups: (1) those that affect the activities of the plants directly, and (2) those that exert an indirect or remote effect, usually through some other factor or factors. The effects of the factors in the first group are more easily differentiated even in their interactions, whereas those in the second group are less easily detected and frequently are overlooked entirely.

1. MEASURING EFFECTIVENESS OF SITE FACTORS

Some of the site factors, such as air temperature, soil moisture, and atmospheric humidity, are constantly operating on a given site; others, such as wind and certain biotic factors, are intermittently present. All of the site factors may be present on any given site. Sites do not necessarily differ in the presence or absence of site factors but in the degree to which each factor is effective. Thus air temperature is a factor of every site, but no two sites are identical in degree of temperature and its distribution throughout the year. In the study of the factors of a given site it is necessary to determine the extent to which each is present in order to relate them individually to the resulting vegetation. Since the time of Humboldt (1805), more or less attention has been given by scientists to the measurement of the factors of site in terms of their magnitude and periodic fluctuation, in order that these measurements may be compared with similar ones made on other areas and at the same time make possible the comparison of the vegetation of the areas. Ecologists and silviculturists in this country, notably research workers at the forest experiment stations, have measured the various factors of site in a number of localities and have attempted to determine the influence of each on the resulting vegetation. As yet, however, there is relatively little information derived from carefully executed field studies on vegetation and the actual measurement of site factors.

2. EFFECT OF SITE FACTORS ON FOREST VEGETATION

The various direct factors of site act upon the elements in the vegetation as external stimuli. Thus a certain degree of heat, by reaching the living plant tissues, stimulates a plant to increased growth. Decrease in the atmospheric humidity in contact with the plant tends to cause increased transpiration. Decrease in light stimulates leaf expansion.

Owing to the varying influence of the site factors, forest vegetation is in a constant state of adjustment. Virgin forests are more or less perfectly adjusted to the site factors; but artificial forests, that is, those regenerated by seeding or planting and those that have been thinned or otherwise modified by man, are usually less perfectly adjusted. When species not indigenous to the site are used in regeneration, the vigor and growth of the artificially established vegetation depend upon how closely the vegetation is correlated with the site factors. They depend upon how closely all the site factors in the locality where the species reaches its optimum development correspond to the site factors where the species is used. The greater the variation in the site factors in one direction or another, the less likely it is that a species will succeed beyond its natural range. Thus the pines of Georgia die when attempts are made to grow them in Connecticut, and the hickories and beech die when attempts are made to grow them in Arizona.

3. COMPENSATING FACTORS

Site factors very commonly supplement each other in their effects on forest vegetation. A forest community may attain excellent growth and development when one or more of the site factors is deficient, provided the favorableness of the others compensates for this deficiency. A favorable climate may induce good growth in an unfavorable soil. Favorable atmospheric humidity may compensate for deficient rainfall. Mesophytes occur along streams in arid regions because the soil contains ample available moisture which compensates for dryness of the air. A southern exposure may compensate for a relatively cool climate.

In general, a plant or a plant community may be considered as one of two interacting systems; the other is environment. The plant community is composed of growth forms in which the individual plants comprise a complex of organs, tissues, and cells. The environmental system is a complex of activating agents. Although the influence of these agents on the community or plant is expressed most clearly in terms of significant factors, it should be emphasized that the limitations that tend to be imposed by unfavorable factors may, within limits, be

offset by the reactive behavior of a plant or community itself, or compensated for by other factors of the environment which are highly favorable.

This principle has sometimes been called the *law of compensating factors.* Thus when a certain reaction in a plant depends upon the combined action of several factors, the reaction tending to be restricted by one of these factors, the limiting effect of this factor, within certain bounds, is beneficially modified by the degree of favorableness of the other factors.

In the ordinary habitats of shade plants, several factors determining the rate of assimilation are all likely to be significant, so that any increase in one tends to compensate for the others. Thus, an increase in chlorophyll-bearing leaf area and thinness of leaf may compensate for reduced light intensity (Lundegårdh, 1922).

As the various site factors are more or less interdependent, it is often quite difficult to determine whether certain conditions of the vegetation are due to one factor or to some other. Because one factor may supplement another, it is often impossible to determine how far the influence of a given factor extends. However, it must be recognized that a given vegetation results from all the site factors working together. It is extremely difficult in any given site to select any one factor, such as air temperature, soil moisture, or soil composition, and to state to what extent the vegetation present is due to its effect.

Available soil moisture has an apparent effect on the light requirements of a given species. Thus, where undergrowth appears to be suffering from lack of light and is revived by increasing the water supply, the poor condition has most likely been brought about by the lack of soil moisture due to root competition rather than to lack of light. The increase in light without increasing the water supply has little effect in stimulating growth. The experiments of Fricke (1904), Fabricius (1927, 1929), Toumey and Kienholz (1931), and others, which have already been discussed, show that soil moisture affects apparent light requirements most when the moisture content of the soil is at or near the wilting percentage and light intensities are high.

The distribution of spruce reproduction in the interior forests of British Columbia, where the annual precipitation is 30 inches or less and where August droughts are of common occurrence, is much more abundant and more thrifty where decayed wood is present beneath the surface litter (Barr, 1930). The decayed wood absorbs large quantities of water during wet periods and retains available water over longer periods of drought than on sites where decayed wood is absent.

Reproduction of hemlock in the upland forests of New England is more abundant and more vigorous immediately surrounding the bases of standing trees forming the overstory and in narrow zones at the periphery of the crowns. It is correspondingly weak and scanty over the intervening areas. This is due to marked differences in available soil moisture. A considerable part of the precipitation reaches the soil immediately surrounding the boles of standing trees by running down the main branches and boles. So also, where the ends of the branches droop, as in hemlock, another considerable part of the precipitation drips from the periphery of the crowns to the soil beneath. The intervening areas between the relatively moist zones surrounding the boles and at the periphery of the crowns receive little of the precipitation. This very unequal distribution of the precipitation accounts for the unequal distribution and vigor of reproduction. Thus, as Zon and Graves (1911) have shown, the poor development of reproduction directly under or near seed trees may be explained, not by shading alone, nor by the mechanical action of water dripping from the leaves and branches of the old trees, nor by excessive light reflected from the trunks, but by the moisture-sapping competition of the roots of older trees. Trees with extensively developed, ramifying, superficial root systems naturally desiccate the upper layers of soil much more than trees with less extensive, deeper root systems.

As with soil moisture, the effect of soil fertility on the light requirements of a species is not readily apparent. When a poor condition of growth under cover is found to be improved by increasing fertility of the soil, the poor growth can be attributed primarily to deficient soil nutrients and not directly to deficient light. A fertile soil apparently enables a tree to grow and develop to such an extent that trees on rich soils, even under deficiencies of light and moisture, appear to be more tolerant than those on infertile soils. It has been shown by Hartig (1891) that, with the same light intensity and available soil moisture, the assimilative energy of trees increases with increase of available soil nutrients. Thus trees on poor soil but in full light may have the same assimilative capacity as the same species growing on good soil but in deficient light.

Competition in forests, as has already been shown, involves a struggle between the component plants in order to satisfy their needs for light, soil moisture, and soil nutrients (Clements, Weaver, and Hanson, 1929).

The presence or absence of certain species, their relative vigor under living canopies, and the extent to which they withstand suppression are now known to be not entirely a question of light requirement. Many

other factors of the site which affect plant survival and growth must be considered in explaining the condition of vegetation on the forest floor. A number of investigators have already recognized the importance of these factors and have pointed out their effect on reproduction, growth, and succession in forests. As early as 1852, Heyer wrote that reproduction in a forest does not fail, even on poor soils, when moisture is adequate. Hartig (1891) states that the growth of trees increases without an increase in leaf area or light intensity if the nourishment of the trees is increased. Mayr (1925) has pointed out that foresters overstress the idea that poor development of trees in dense stands is due to weak light intensity. They neglect to take into account the decrease in available soil moisture and the deficiency of nutrients. He states that root competition may be keener than crown competition. When trees and other vegetation, growing under dense natural canopies, are freed from root competition, they respond by more rapid growth. Where the surface soil is bare of all vegetation beneath dense living canopies, it almost immediately becomes covered with surface vegetation when released from root competition (Fricke, 1904; Toumey, 1929; Korstian and Coile, 1938).

Both the vegetation and soil are dynamic over the period of development of a forest (Toumey, 1930). The various climatic, edaphic, physiographic, and biotic factors, outlined in the preceding chapters, make up the environmental complex under which seeds and plants grow and develop. In relating this complex to the vegetation, it has been assumed that for each separate function in a given element in the vegetation there is an optimum condition in one or more factors, such as light, temperature, and moisture. Therefore, for each plant there is an optimum environment to which all its functions are most harmoniously adjusted. Optima in the various factors, however, do not adequately explain the relation of trees and other plants to their environment. Such relations are better explained in terms of the most significant factors.

4. MOST SIGNIFICANT FACTORS

Even though the various factors of the site supplement each other within certain, although ill-defined, limits, and the vegetation is the result of their combined action, a single condition such as soil moisture may be the most significant factor as far as a given type of plant community is concerned. In accounting for plant communities in terms of site factors, the variable factors which at times fall short of the communities' requirements are of prime importance. Thus

in accounting for the plant communities within a climatic type, climatic factors are essentially constant in their action and need not be taken into account. On the other hand, in accounting for the differences in climax vegetation of adjacent climatic types the climatic factors are unlike and are consequently critical factors of great importance. Within a given climatic type the most significant factors are chiefly edaphic, physiographic, or biotic.

The problem of significant factors is greatly simplified if the most important factors for any given time and site can be determined.[1] Baker (1934) aptly states that "factors are important when present in critical concentration, when almost any factor may assume an enormous importance, far outweighing all others." Thus moisture may be critically significant during droughts, wind during storms, and temperature during severe cold periods. The *law of the minimum* materially assists in understanding the relative importance of the various site factors. This law, in its older form as developed by Liebig (1855), may be stated as: "*When a process* [such as assimilation] *is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor.*" (Blackman, 1905). Thus, when a pine tree assimilates under increased light intensity, the rate of assimilation rises until a certain point is reached. No further rise occurs with further increase in light intensity. At this point, however, some factor other than light, such as temperature or available moisture, becomes most significant, and further increase in light intensity is non-effective. If, however, the factor that becomes most significant is increased, it is found that, with further increase in light intensity, the rate of assimilation continues to increase. Whichever of the factors affecting assimilation is least favorable (in minimal amount) will determine the rate.

Liebig's law of the minimum has been restated by Mitscherlich (1909, 1921) as "*The increase of crop produced by unit increment of the lacking factor is proportional to decrement from the maximum*" (Russell, 1932). His restatement of the law implies that the growth factors which are present in minimal amounts are most important in governing the growth rate and size of crop. Of even greater importance are the deductions that the yield of a crop depends on the integrated effect of

[1] Where adequate quantitative data are available, the determination of the relative importance of two or more factors, which influence biological phenomena to varying extents, is greatly facilitated by the application of certain methods of statistical analysis used to indicate degree of correlation and relative significance of variables.

all the site factors and that the factor farthest from its optimum concentration will be most effective in reducing the yield, but it alone will not determine the yield (Baker, 1934). It must be considered along with the other factors.

The term *limiting factor* has been introduced to denote a factor which by its insufficiency or excess may prevent other factors from exerting any pronounced effect upon plant growth (Blackman, 1905). Although this term has an established place in forest ecology, a single factor seldom becomes limiting in a forest. The vegetation on any given site is generally the resultant of a complex of environmental factors. When the absence of a particular vegetation is accounted for by one factor's becoming limiting, invariably other factors, either directly or indirectly, play an important part in determining at what point the so-called limiting factor actually becomes most significant.

The early investigators, whose work is reviewed by Stiles (1925), reached the conclusion that, when other factors are not more significant, the rate of photosynthesis is proportional to light intensity. Because of faulty methods in measuring the light intensity and rate of photosynthesis, however, these early experiments were unreliable. Blackman and Matthaei (1905), working with less faulty methods, arrived at their " Principle of Limiting Factors," which is essentially the same as Liebig's " Law of the Minimum." They conclude that when a process is dependent upon a group of two or more factors, the rate of the process is determined by that factor which is available in relatively smallest amount.

Romell (1926) has pointed out the defects in the law of limiting factors as applied to vegetation. He argues that a static law cannot be applied to a dynamic process such as the growth and development of vegetation. The propriety of using the term " limiting factor " has also been challenged by Allen (1929). He suggests the term *most significant variables* for those factors which are far from their optimum and whose effect is therefore disproportionately great, for, as he states, the " individual factors in a natural environment are not clearly separable." It seems preferable, however, to use the term *most significant factors* when referring to a forest environment. In resolving the environment into its simpler components and in correlating these components with each other and with plant growth, mainly for the purpose of determining their biological significance, it is desirable to refer to them as factors rather than variables.

In a thorough review of the rôle of light in the life of plants with particular reference to its influence upon physiological processes,

growth, and differentiation of plants, Burkholder (1936) makes the following significant statement:

> The physiological activities, characteristic growth, and differentiation of plant species are brought about by the interaction of all the many factors of inheritance and environment. No one factor taken alone and divorced from all other contributory conditions, such as light, temperature, moisture, minerals, etc., can be considered as being significant in the life of plants. All variables work together and each shares to a greater or lesser extent in the different processes which determine the morphological destiny of the growing plant. Along with other components of the environment, light is known to have profound effects upon the properties of matter and it should be expected, therefore, to have an important influence upon living organisms.

In discussing light as an ecological factor Shirley (1935) aptly points out that, for a proper evaluation of the effect of light on the growth of plants in natural forest habitats, an understanding of the many other factors influenced by forests is necessary. By way of illustration, he refers to reduction of wind velocity and air temperature, although the air temperature may sometimes be higher in small openings, particularly when cool winds are blowing. Also evaporation is decreased and a number of other factors changed.

Most site factors have both a minimum and a maximum value. Thus with heat intensity, if the temperature is lowered a point is finally reached at which a given vegetation or plant is killed. If the temperature is raised a point is also reached at which it is killed. Life is retained only at temperatures which fall between these limits. This principle is known as the *law of physiological limits*. In accordance with this law, life persists in any particular organism only so long as environmental conditions do not surpass the physiological limits imposed by the life processes of the particular organism.

5. MODIFICATION OF SITE FACTORS IN SILVICULTURAL PRACTICE

Knowledge of the most significant factors is important in the practice of silviculture. A forester should so control stand composition, stand density, and regeneration as to bring about the most desirable forest conditions for optimum yields, watershed protection, game cover, aesthetic effects, or any other objects of management that may be prescribed for his forest.

In far northern regions the most significant factor in timber growth often is the temperature of the soil. This can be increased by opening stands and exposing the soil to a larger amount of direct sunlight. The factor most likely to inhibit reproduction and survival under

natural canopies is available soil moisture. This can also be increased by opening the stands and by reducing the intensity of competition for soil moisture between the canopy trees and the subordinate vegetation. In general, the yield possibilities of a given site are determined by its most unfavorable factor. The improvement of this factor is the first step that a forester should take in order to make his forest more productive.

When light is the most significant factor, it appears that, although each species must receive a certain intensity of incident light in order to survive, the rapidity with which dry matter is accumulated in a plant under each added increment of light varies widely in different species and under different environmental conditions. Thus, when a forest is opened by a thinning, which reduces stand density, the vegetation beneath the crown canopy not only receives more light but, among other things, is subjected to increased temperature and moisture. Species in the subordinate vegetation respond differently to thinning, because of their different abilities to assimilate CO_2 under increased temperature, moisture, and light.

The essential photosynthetic differences between species subjected to added increments of light above the minimum appear to be in their having different coefficients of increase in assimilative activity with change in available moisture, soil nutrients, and temperature, as well as the other factors in the environment which accompany change in light intensity under living canopies.

Because trees growing in the open blossom and fruit earlier and more abundantly than the same species growing in dense stands, it has been assumed that greater light intensity is required for these functions than for vegetative growth. The important reason for preparatory or seed cuttings under certain silvicultural systems of natural regeneration is to open the crown cover so as to admit more light to the trees in the remaining stand in order to stimulate seed production. However, other factors may also be effective. For instance, the increase in blossoming and seedage may be due to diminished competition and to more abundant soil moisture and nutrients, bringing about an increase in available synthesized carbohydrates. Seed production is stimulated by conditions favoring a carbohydrate reserve.

A dense stand tends to lower temperature, to lower soil moisture during dry periods, to slow down decomposition of litter, to lower evaporation, and to increase soil acidity in coniferous stands. Soil microorganisms are distinctly influenced by stand density, but are even more influenced by stand composition. The macrofauna of soil under

dense spruce stands in Saxony is greatly increased in number as a result of converting the stands to mixed conifer-hardwood forest. Such a change has a marked effect on all vegetation on the forest floor.

Density of the overstory affects both reproduction and other understory vegetation through competition of roots for soil moisture and nutrients. Density of shrubby and herbaceous vegetation likewise affects the possibilities of obtaining natural reproduction and, to a marked degree, determines the animal life which can exist within a forest. The lack of undervegetation in many European forests is due more to excessive grazing by game animals than to excessively high density of overstory.

Where a stand supports a very luxuriant undergrowth it is positive evidence that the overstory is not completely utilizing the site. Both light and soil conditions are sufficiently favorable to support the understory vegetation. Furthermore, if a stand of pine in the Lake States and in many parts of the eastern and southern United States is invaded by a dense understory of shrubs it is almost impossible for natural reproduction of pine to follow any type of cutting unless cleanings are made in which pine reproduction is favored. It may even be necessary to supplement natural regeneration by the planting of pine followed by cleanings.

The failure or decline of reproduction under an old stand may be due to root competition for soil moisture and to other factors, and not to the shading effect of the overstory. It appears that the so-called "light increment," or increase in growth after thinnings, may not be due to increased light but largely to less root competition for soil moisture and to favorable changes in other physical factors. Although thinning permits additional light to reach the interior of a stand, the chief effect is in reducing competition, which leads to an increase in soil moisture. As already indicated, leaf litter is also more readily decomposed in thinned than in unthinned, fully stocked stands. Thus the soil under thinned stands becomes enriched with nutrients, which results in increased growth following thinning.

Competition of low shrubs and herbs which are in the same crown level and also at the same root level as planted trees has been responsible for widespread failure in plantations in parts of the western United States and in the Lake States. In times of severe drought, as during the summer of 1936 in the Lake States, losses are low where no surface vegetation occurs and planted trees are exposed to uninterrupted direct insolation. This suggests that soil moisture is the factor that becomes most significant in such situations and that it should be con-

served as much as possible. The reduction in competition as a result of furrow planting practiced in the sandhills of Nebraska and the relatively high survival of the shelterbelt planting during the severe drought of 1936, attributed almost entirely to intensive soil cultivation, point to available soil moisture as the critical factor. The conservation of soil moisture and the maintenance of a favorable moisture reserve, or balance between supply, absorption, and loss of water, may often determine the difference between failure and successful survival of plantations and even stands of natural reproduction. The elimination of unnecessary competition from shrubby and herbaceous vegetation, especially during times of water shortage, may be an essential requisite to satisfactory survival of forest trees on many potential forest lands.

In the application of silvicultural measures throughout the entire life of a forest stand — from the first step taken to stimulate seed production and the reseeding of an area, through subsequent cleanings, thinnings, and other care of the stand, to the establishment of the next crop of reproduction — a practicing forester should at all times endeavor to maintain environmental conditions favorable to optimum growth and development of his forest in accordance with the objects for its management.

PART II

INFLUENCE OF FORESTS ON THEIR ENVIRONMENT

CHAPTER XI

REACTION OF FOREST VEGETATION ON ITS PHYSICAL ENVIRONMENT

1. REACTION CONCEPTS

Forest vegetation reacts on its environment in a direct and positive manner. The term *reaction* as here used relates to the effect that a forest community exerts on the physical factors of site (Weaver and Clements, 1929). The direct reactions of a forest are confined largely to reactions on physical factors such as air temperature, wind, soil moisture, and soil nutrients; however, the reactions of a forest on the biotic factors are also important.

The development of a forest community from the first isolated individuals that occupy an otherwise bare site to a climax forest is largely the result of reaction of plants and animals on a site. Development results from a series of progressive reactions which terminate in stabilization of vegetation.

The indirect value of forests is due to reaction. The term *forest influences* is often applied to the effect of forests on site factors (Fernow, Harrington, Abbe, and Curtiss, 1893). The influence of forests upon microclimate, upon the supply and distribution of water, upon soil, and even upon man himself is of great importance.

Although the reactions of forests on climate, soil, and man have been observed from the earliest times, the number of factors which make up these reactions is so large, the difficulty in accurately observing them so great, and the economic interests affected by them so diverse that there has been a wide divergence of opinion on the entire subject (Zon, 1913, 1927).

The beneficial reactions of forests are due primarily to:

1. The unbroken canopy of a fully stocked stand at a variable distance above ground intercepting the sun's rays and precipitation. It also checks wind velocity and retards loss of heat by radiation.
2. Organic material such as leaves and other forest litter, supplied annually

to the soil by a stand of growing timber and lesser vegetation, a layer which protects the soil and greatly influences its relation to water and air, and increases soil fertility.

3. The continuous expanse of interlaced roots of a fully stocked stand binding the soil together and at the same time rendering it more porous (Schlich, 1896).

When the older literature on forest influences is examined it is observed that the outcries against disastrous effects of deforestation on climate and soil always occurred during dry or warm periods. It is also found that the favorable effect of afforestation is chiefly emphasized during wet periods. Because of periodicity in climate it is not safe to compare temperature and rainfall of one year with that of another and claim that the difference is due to differences in forest vegetation. This is illustrated by observations made in Australia. In 1870 the opinion prevailed that deforestation was resulting in desiccation of the country. This date proved to be at the height of an exceedingly dry period. In 1880 the same people were convinced that deforestation caused a decided increase in humidity. This date proved to be at the height of an exceedingly wet period.

2. CLASSIFICATION OF FOREST REACTIONS

In a general way forest reactions may be classified relative to reaction of forest vegetation on:

1. Climate.
2. Soil.
3. Animal life and man.

Although researches made at comparable stations and evidence obtained by historical inquiry have had for their object the solving of problems relating to forest reactions, scientific methods of research have been chiefly confined to studies of effect of forest vegetation on:

1. Air temperature.
2. Soil temperature.
3. Atmospheric humidity.
4. Precipitation.
5. The conservation of water.
6. Air currents.
7. Avalanches.
8. The soil.
9. Animal life and man.

3. EFFECT OF FOREST VEGETATION ON AIR TEMPERATURE

Although there is considerable variation in the data obtained at different localities and at different times, the evidence is conclusive

that forest vegetation reduces mean annual temperature 5 feet above ground from 0.8 to 1.8° F., depending upon character of forest and locality, particularly elevation. The effect of a forest in reducing temperature is much greater 5 feet above ground than in the tree crowns. Schlich (1896) states that the general average of many stations is as follows:

Five feet above ground	1.01° F.
In the tree crowns	.41° F.

The following table, compiled by Zon (1927) from European sources, is a summary of the data from stations in 5 countries. It brings out clearly the moderating influence of forest vegetation on air temperature. The signs + and – indicate that the temperature in forests is respectively higher and lower than in the open.

DIFFERENCES IN TEMPERATURE OF AIR IN FOREST AND IN OPEN

Period	Central Italy	Eastern France	Mountains of Alsace	Bavaria	Eastern Prussia
	Deg. F.	*Deg. F.*	*Deg. F.*	*Deg. F.*	*Deg. F.*
February–April:					
Average of daily maximum	......	–1.44	–1.98	–0.90	–1.26
Average of daily minimum	......	+1.44	+3.42	+ .36	+ .18
Mean temperature	......	......	– .72	– .54	– .54
May–July:					
Average of daily maximum	–7.38	–5.76	–4.50	–3.96	–2.52
Average of daily minimum	+2.88	+2.16	+3.42	+1.98	+ .90
Mean temperature	–2.16	–1.80	– .54	–1.62	– .72
August–October:					
Average of daily maximum	–6.48	–4.68	–3.42	–5.76	–2.88
Average of daily minimum	+1.98	+2.34	+4.32	+2.88	+ .36
Mean temperature	–2.34	–1.08	– .36	–1.44	–1.26
November–January:					
Average of daily maximum	......	–1.62	+1.62	......	– .54
Average of daily minimum	......	+1.08	+3.06	+2.16	– .36
Mean temperature	......	– .18	+2.34	+1.08	– .36
Entire year:					
Average of daily maximum	......	–3.42	–2.26	–2.70	–1.80
Average of daily minimum	......	+1.80	+3.60	+1.80	– .36
Mean temperature	......	– .72	+ .72	– .54	– .72

The second table compiled from observations in Bavaria and Würtemberg shows the range of air temperature during the 24 hours.

DIFFERENCES IN MEAN TEMPERATURE BETWEEN FOREST AND OPEN COUNTRY AT 5 FEET ABOVE GROUND IN DEGREES F.

Season	Minimum at night	8 A.M.	Maximum early afternoon	5 P.M.
Spring	+ .81	−1.82	−3.87	−2.09
Summer	+3.15	−3.42	−7.42	−3.44
Autumn	+2.59	− .99	−4.00	−1.06
Winter	+ .95	+ .27	−1.96	− .99
Mean of year	+1.87	−1.49	−3.91	−1.89

The above tables show that air temperature is not only lowered by a forest but it is subject to much less fluctuation, particularly in daily extremes. The greatest influence of forests on air temperature occurs in warm regions.

The following table derived from Prussian observations (Schlich, 1896) shows the extent to which species influence the effect of vegetation on air temperature.

Species	Reduction of highest temperature in July	Increase of lowest temperature of January
Beech forest	−8.37	+2.12
Spruce forest	−4.61	+4.28
Scotch pine forest	−4.14	+2.12

It would appear from this table that beech has far greater influence in summer than spruce and pine but less than spruce in winter. This, however, should be expected, because of the dense foliage of beech in summer and its leafless condition in winter.

Researches conducted by Li (1926) in the Yale Demonstration and Research Forest, near Keene, New Hampshire, show the effect of fully stocked 30-year-old and 60-year-old white pine stands on air temperature 3 feet above the surface. Comparison was made with the temperature at the same height above the surface on a nearby area of the same elevation which was denuded of all vegetation.

TEMPERATURE DIFFERENCE BETWEEN DENUDED AND FOREST STATIONS

	Young forest station				Old forest station			
	July	Aug.	Sept.	Oct.	July	Aug.	Sept.	Oct.
Maxima	−4.71	−4.46	−4.10	−3.47	−4.86	−4.27	−3.95	−2.97
Minima	+3.17	+2.68	+2.37	+3.61	+3.17	+2.60	+2.45	+3.93
Mean	− .77	− .89	− .86	+ .07	− .85	− .83	− .75	+ .48

MEAN DAILY RANGE OF AIR TEMPERATURE

	July	Aug.	Sept.	Oct.
Denuded station	37.42	32.89	31.45	38.24
Young forest station	29.54	25.75	24.98	31.16
Old forest station	29.39	26.02	25.05	31.34

DIFFERENCE BETWEEN MEAN DAILY RANGE IN DENUDED AND IN FOREST STATIONS, IN DEGREES F.

	July	Aug.	Sept.	Oct.
Young forest station	−7.88	−7.14	−6.47	−7.08
Old forest station	−8.03	−6.87	−6.40	−6.90

Concurrent conclusions of various investigators on the effect of forests on air temperature are:

1. Forests lower the daily mean temperature in spring and summer and raise it slightly in autumn and winter.
2. Forests lower the daily maximum of air temperature and raise the daily minimum. This effect is more significant in summer than in other seasons.
3. Forests diminish the daily range of air temperature. This effect is most significant from May to October.

Pearson (1914) found that there was a difference of 6.4° F. between the mean minimum temperature of forested and open areas, the latter having the lower range. The mean maximum was about 1° F. higher in the forest. A comparison of minima in the forest and in a cut-over area of the same topographic situation showed a mean of about 2° F. lower in the clearing. He concludes that radiation is partly responsible for the lower minima of the open and also that cold air drainage is

partly responsible. The mean summer temperature of the soil at a depth of 2 feet was about 5° F. higher in the open than in the forest. The mean humidity of summer was approximately 2.5 percent higher in the forest and that of winter about 3.5 percent higher in the open. The influence of differences in climate in the forest as compared with the open is reflected in the fate of 2-year-old pine seedlings planted on the two sites. Ninety percent of those planted in the forest survived at the end of one month of arid, windy weather, whereas but 11 percent survived in the open.

Woeikov (1885) has published a series of tables to show the effect of forest vegetation on temperature of the surrounding country. He shows that in Europe temperature rises in proceeding from the Atlantic coast eastward to continental countries, but that the steady increase is here and there interrupted, owing, he believes, to the presence of large bodies of timber, and their effect upon water which escapes into the air through transpiration and evaporation. In this and similar cases, however, it is impossible to state to what extent other circumstances may have caused the interruptions.

Geiger (1927) has investigated the variations in air temperature in forest stands at various hours of the day and at various elevations from the soil surface to a distance above the canopy. In midsummer, at midday, he found in a fully stocked stand that air temperature was lowest at the soil surface and became progressively higher above the surface to approximately midway between the ground and the base of the canopy. From here, it became gradually lower well into the canopy and then rather rapidly higher and considerably higher immediately above the tree crowns. The cooler temperature in the canopy than midway between the canopy and the ground is due to higher wind velocity and to some extent to transpiration from the foliage which cools the air.

4. EFFECT OF FOREST VEGETATION ON SOIL TEMPERATURE

Forest vegetation has the same effect on soil temperature that it has on air temperature, only in greater degree. The surface layer of soil is heated directly by the sun, but the air receives its heat for the most part from the soil. For this reason the difference between temperature of the upper layer of soil in a forest and in the open is especially marked. Although the difference is greatest in the surface layer of soil, it is manifest at a depth of 4 feet or even more.

In the main, temperature of the soil in its upper layer follows in its variations the changes in air temperature. As the temperature of soil

below its superficial layer is fairly uniform throughout the day, it affords an excellent means for measuring the average effect of forest cover. The following tables compiled from European observations show the differences in soil temperature, the fluctuation in soil temperature, and the effect of different species on soil temperature inside a forest and in the open:

DIFFERENCES IN MEAN SOIL TEMPERATURES INSIDE AND OUTSIDE FORESTS

	February-April		May-July		August-October		November-January		Mean Annual	
	At surface	At a depth of 35.4 inches	At surface	At a depth of 35.4 inches	At surface	At a depth of 35.4 inches	At surface	At a depth of 35.4 inches	At surface	At a depth of 35.4 inches
	deg. F	*deg. F.*	*deg. F.*	*deg. F.*	*deg. F.*	*deg. F.*	*deg. F.*	*deg. F.*	*deg. F.*	*deg F.*
Mountains of Alsace	−1.88	+0.90	−14.04	−5.04	−10.26	−5.76	+0.54	−1.26	−6.30	−2.70
Bavaria	−3.24	−1.44	− 8.10	−7.02	− 4.68	−5.40	.....	− .18	−3.96	−3.96
Bavaria	−2.30	−1.08	− 8.28	−7.38	− 4.68	−5.40	+ .54	− .18	−3.78	−3.60
Eastern Prussia	−2.34	.....	− 7.92	−6.48	− 4.14	−3.96	+2.34	+1.62	−2.88	−2.16

The above table, compiled by Zon (1927), shows that the winter temperature of soil in a forest and in the open differs but little. On the whole, the winter temperature is slightly higher in the forest. When snow lies on the ground several months each year it is considerably higher. The summer temperature, on the other hand, is much lower in forest soil. Soil in a forest is cooler in spring and warmer in autumn. On the average, forest soil is about 1.8° F. warmer in winter and from 5 to 9° F. cooler in summer than soil in the open.

DIFFERENCE IN TEMPERATURE OF SOIL INSIDE AND OUTSIDE A FOREST, ACCORDING TO SPECIES

Season	Spruce	Beech	Larch
	Deg. F.	*Deg. F.*	*Deg. F.*
Spring	−5.72	−2.47	−2.02
Summer	−9.18	−6.43	−4.88
Autumn	−4.10	−2.99	−2.56
Winter	+ .16	− .16	+ .59
Mean of year	−4.81	−3.01	−2.21

The above table, derived from Swiss observations extending over a period of 12 years, shows that spruce reduces soil temperature much

more than beech, a deciduous species, and still more than larch, which not only is deciduous but has thin, open foliage.

European observations have shown that mean annual soil temperature is, at all depths down to 4 feet, lower in a forest than in the open, and that this difference is greatest in summer and least in winter. The mean annual difference at a depth of 2 feet is 1.9° F. in Prussia, 3.5° in Bavaria, and 3.2° in Württemberg (Brown and Nisbet, 1894).

Observations made in the United States, although not so complete as those recorded in Europe, in general substantiate the European conclusions. Pearson (1914), working in northern Arizona, found that from July 1 to October 30, 1911, soil temperature at a depth of 2 feet averaged 54.25° F. in a ponderosa pine forest, and 5.1° F. higher in the open.

Li (1926) has studied temperature of surface soil at depths of 6, 12, and 24 inches in 4 sites near Keene, New Hampshire. All 4 sites were similar with the exception of their vegetation cover. The first was entirely denuded of vegetation; the second sustained a grass cover; the third supported a 30-year-old, fully stocked stand of white pine; and the fourth a white pine stand 60 years old. He found that forests greatly lower soil temperature from July to October, particularly at the surface. Thus the mean maximum surface temperature on the denuded site was 118.8° F., for July, whereas it was only 65.1° F. for the same month in the younger pine forest. The mean daily range between maximum and minimum was 66.0° F. in the open and but 31.4° F. in the forest. The effect of the 30-year-old forest on maximum surface temperature reached in July was to lower it 33° F. The effect on the minimum was to raise it 3.5° F. The effect of forest on surface temperature was subject to extreme fluctuation due to changes in current climatic conditions, especially cloudiness. The decrease in daily maximum during the growing season due to forest varied from 5.5 to 67° F. The increase in daily minimum due to the same cause varied from 0 to 19° F. On warm, cloudy nights minimum surface temperature of denuded soil is higher than that in the forest. The daily range of surface temperature is greatly reduced by a forest, particularly in summer. This reduction may be as great as 50 to 60° F. The effect of a forest in raising minimum surface temperature was mainly due to the presence of litter, and the trees exerted little or no influence in this respect. The effect of a forest in lowering maximum surface temperature was largely due to the presence of a tree canopy, and the effect of litter was slight. It has been found that in a pure pine stand in northern New England 77.7 percent of the reduction in maximum was due to the canopy and 22.3 percent to litter. The effect of a forest, although

greatest in reducing daily range at the surface, is apparent to depths of 2 feet or more. A 60-year-old stand of white pine reduced average daily range in July, at a depth of 6 inches, between 5 and 6° F. At a depth of 2 feet the effect of forest on daily range was reduced to a small fraction of a degree.

The influence of forest vegetation on freezing of the soil is of great importance, as shown from 21 years of observations by Schubert (1900) in Germany. His observations show that soil under a forest usually remains soft when that in the open is frozen to considerable depth. They also show that when forest soil freezes it is only to a depth of one-half to less than three-fourths that in the open. Thus at Eberswalde, Prussia, when sandy soil mixed with humus froze to an average depth of 27.6 inches in the open, it froze to a depth of only 18.5 inches under stands of Scotch pine.

In northern Arizona Pearson (1914) found that on February 18, 1913, soil on the north side of trees in a ponderosa pine forest was frozen from the surface to a depth of 13.5 inches, and on the south side every trace of frost had disappeared, while in a large, nearby open area soil was frozen from the surface to a depth of 29 inches.

Studies made at New Haven, in 1926–27, show the effect of forest litter on soil freezing. The ground did not freeze until January under a 20-year-old stand of red pine, having leaf litter approximately 2 inches thick. Under a part of the same stand where the litter was removed, the surface soil froze on November 13, and water from heavy rains that followed a few days later flowed over the surface with none of it percolating into the soil. On the other hand, on that part of the area where the litter was intact, none of the water flowed over the surface, but all was taken up by the soil.

The surface soil froze solid on the area with the litter removed and remained frozen until spring. After January 1, however, when the ground froze under litter, the freezing was of an entirely different character. The soil did not freeze solid but contained numerous holes and irregular openings into which the water could pass freely. Other studies in the same locality showed comparable beneficial effects of forest litter on soil temperature and soil freezing (Korstian, 1927; MacKinney, 1929).

5. EFFECT OF FOREST VEGETATION ON ATMOSPHERIC HUMIDITY

Living plants transpire as long as the vegetation is alive. Transpiration from them causes air below the uppermost part of the canopy to

have a relative humidity much higher than corresponding layers in the open or under dead vegetation. The taller the vegetation, the greater its effect. So also, the greater the area of transpiring leaves in a given air layer, the greater the relative humidity in that layer.

The average of available observations shows that forest vegetation does not affect absolute humidity of the air to an appreciable extent. This is well brought out in the results of Bavarian observations as shown in the following table.

MEAN ABSOLUTE VAPOR TENSION IN INCHES

	In the open, 5 feet above ground	In a forest, 5 feet above ground	Excess in the forest
Spring	0.2788	0.2824	+0.0036
Summer	.4626	.4618	− .0008
Autumn	.2806	.2886	+ .0080
Winter	.1820	.1918	+ .0098
Mean of year	0.3010	0.3064	+0.0054

There appears to be considerable difference in the saturation deficit of forest air and that in the open. This difference is greatest in summer and least in winter. There is no appreciable difference in the spring months in regions of heavy snows due to their melting. The following table compiled by Zon (1927) shows the relative humidity inside and outside forests at three localities in Europe. It shows the effect of forest for different seasons and for the entire year.

RELATIVE HUMIDITY OUTSIDE AND INSIDE FOREST IN PERCENTAGE OF SATURATION

	February-April		May-July		August-October		November-January		Entire year	
	Outside forest	Inside forest	Outside forest	Inside forest	Outside forest	Inside forest	Outside forest	Inside forest	Outside forest	Inside forest
Mountains of Alsace	80	85	68	75	78	84	85	89	77	84
Bavaria	80	84	70	80	78	85	87	90	79	85
Eastern Prussia	84	85	64	68	76	81	90	92	78	82

The difference in relative humidity inside a forest as compared with

the open is usually from 3 to 10 percent. In some cases it may be as much as 12 percent.

Geiger (1927) in his researches learned these things about the daily range in relative humidity over the crowns and in the interior of a stand. From shortly after midnight to daylight, when temperature is at its minimum, relative humidity is highest, the different air layers being nearest to saturation, both above the crowns and in the interior of a stand. In general, the differences in relative humidity at this time, both above and within a stand, are very little, usually but 1 or 2 percent. As the sun rises, relative humidity progressively decreases until about 2 p.m., when it may be 20 to 40 percent lower, and 3 or 4 percent lower in the forest than above the tree crowns. The daily minimum both in a stand and above the tree crowns is raised when temperature is at its maximum about 2 p.m. From this time, the difference in relative humidity over and under a stand progressively increases to its maximum of about 10 percent at sundown. From about 2 p.m. until sundown, there is a rather rapid increase in relative humidity both over and under the stand. From sundown until midnight the increase is much less rapid. The general trends in relative humidity, both above and under the canopy, as herein stated, are greatly modified by time of year, climatic regions, weather conditions, and nature of the stands.

The effect of forest vegetation on relative humidity of the air appears to vary considerably in different localities, more particularly with differences in elevation. The Bavarian observations show a difference of but 3.14 percent at 1,066 feet above sea level and 8.79 percent at an altitude of 2,956 feet. The effect of forest vegetation also varies with the species as shown in the following table compiled from Swiss and German observations:

EXCESS OF RELATIVE HUMIDITY IN FOREST OVER THAT IN THE OPEN, IN PERCENTAGE OF SATURATION

	Beech	Spruce	Scotch pine	Larch
Spring	+1.91	+6.92	+2.93	+2.83
Summer	+9.35	+8.56	+3.87	+7.85
Autumn	+4.07	+7.01	+4.24	+5.45
Winter	+1.73	+4.76	+2.70	+ .34
Mean of year	+4.27	+6.81	+3.42	+4.12

To what extent forest vegetation affects relative humidity of the air

outside a forest is not known from direct proof. Zon (1913) contends that forests, by increasing evaporation and transpiration at the expense of surface runoff, enrich the passing air currents and in this way help to carry additional moisture into the interior of continents. He concludes that 78 percent of all precipitation over the peripheral land area is supplied by the area itself, and that the amount supplied is largely dependent upon forests.

6. EFFECT OF FOREST VEGETATION ON PRECIPITATION

To what extent forest vegetation influences precipitation is not definitely known. Elaborate studies have been undertaken and much has been written on this subject but the problem is yet mostly unsolved, and no one can say authoritatively that forests appreciably increase the total amount of precipitation.

It would seem that as the air of forests is cooler and moister than air in the open, forests should have some influence on precipitation. On the other hand, precipitation depends chiefly upon wind currents and other powerful agencies, compared with which the influence of forests must be very small.

Precipitation reaches the ground and becomes available for vegetation and stream flow in the following forms:

1. Rain, snow, sleet, and hail.
2. Dew and hoar frost.

The first group forms in the upper strata of the air and is brought to the earth by gravity. The second is condensed directly on the vegetation and on the surface and in the surface soil when it is colder than the surrounding air.

The great difficulty in arriving at a safe conclusion as to the effect of forest vegetation on precipitation arises from the difficulties in establishing rain gauges at two stations under identical conditions with the exception of forest cover, and the natural unevenness of precipitation at nearby stations that appear to be similar in their physical surroundings. Elevation above sea level influences the amount of precipitation. As air cools in rising, precipitation increases with increase in altitude.

Although the comparison of numerous observations of precipitation, at stations within and outside forests in various parts of the world, show conflicting and extremely variable results, the balance of evidence appears to favor the contention that forests increase precipitation,

though to what extent is very uncertain. The effect of forest vegetation on precipitation relates to its effect on:

1. Local precipitation.
2. General precipitation.

7. Effect of Forest Vegetation on Local Precipitation

Observations on the influence of forest vegetation on local precipitation have been under way in various parts of the world for nearly 80 years. Some of these observations show no essential difference in precipitation over forests and in the open. The larger percentage, however, gives a greater precipitation over forests, the excess varying from 1 to nearly 50 percent.

The Prussian observations (Schlich, 1896), extending over a period of 10 years, show increased rainfall over forests, as compared with that taken at 192 ordinary meteorological stations in the open and in the same general locality, as follows for different elevations:

Between sea level and 328 feet altitude	1.25 percent
Between 328 and 556 feet altitude	14.2 percent
Between 1,969 and 2,297 feet altitude	19.0 percent
Between 2,297 and 2,625 feet altitude	43.0 percent

It appears from the above that the influence of forests in north Germany at low elevations is negligible but that their influence increases rapidly with increase in elevation, particularly in mountainous regions.

Angot (1895) brings out in a striking manner the contention that bare mountains do not always cause moisture-laden winds to precipitate their moisture. Although he has no means of absolute proof, he contends that forested mountains increase precipitation with increase in elevation to a much greater degree than denuded mountains.

Weber (1903) compared rainfall data for a period of 7 years at a station in a small pasture surrounded by large forests, near Nancy, France, with precipitation at a station at the same elevation in a nearby region practically without forests. Precipitation at the station surrounded by forests was considerably more than at the station in the open, but varied with the season as shown in the following table:

February, March, April	7 percent
May, June, July	13 percent
August, September, October	23 percent
November, December, January	21 percent

Observations tend to show that the effect of forests on precipitation

varies with the species, coniferous trees having a greater influence than broadleaved species. According to Henry (1901) the greater concentration of vapor over conifers is probably due to the crowns' intercepting a greater amount of precipitation and returning it to the atmosphere.

Observations on the steppes of southern Russia where 5,000 acres of forest were established in an entirely open country are of extreme interest. Forests were established between 1845 and 1863. Two stations, one over a forest and one outside, were established in 1892. During the period 1893–97 precipitation over the forest was 23.9 percent more than in the open. The Bavarian observations and others made elsewhere within recent years show much less influence of forest vegetation on local precipitation than is indicated by the above data.

The condensation of vapor on leaves, branches, and other exposed parts of trees and its later dripping to the ground add to the annual precipitation. In the late afternoon and evening of October 30, 1916, a dense fog prevailed at New Haven, Connecticut. Although there was no rain the ground under trees was thoroughly wet the next morning. Small shallow pools of water 1 to 2 feet in diameter were frequent on sidewalks and pavement under trees. It is estimated that from 0.05 to 0.1 inch of precipitation reached the ground under the trees on that date by condensation and dripping from the branches.

Pearson (1914) in a comparative study of climatic conditions in a pine forest and in an adjacent open area at an elevation of 7,200 feet in northern Arizona found substantial differences in all climatic conditions except precipitation.

8. Effect of Forest Vegetation on General Precipitation

During recent years much discussion has centered around the effect of forest vegetation on precipitation over vast areas, often miles in extent. The contention has been made that this effect of forests on precipitation is far greater than their local effect. Although meteorological data can not as yet be assembled to prove that such a relation exists, theoretical considerations point to an influence of forests on precipitation over vast regions of non-mountainous country. Zon (1913) points out that in the southeastern United States, as soon as moisture-laden winds from the Gulf of Mexico reach the land, they are cooled and begin to lose part of their moisture, but as they move to the northwest they become drier and precipitation decreases. If precipitation over the land depended entirely on the amount of water brought by the prevailing winds from the Gulf, abundant precipitation would be confined to a narrow belt close to the sea. Brückner (1905) has

pointed out that it is evaporation from the land that supplies the atmosphere with moisture for precipitation even more than evaporation from the sea. Forest cover profoundly influences evaporation of water from the land. When the cover of vegetation is more abundantly developed, moisture is returned to the air more rapidly through evaporation and transpiration combined, and the larger is the amount available for reprecipitation farther inland. Zon contends that in our own Southeast, if winds in their passage to the north, northwest, and northeast did not encounter forests bordering the coast and after precipitation were not enriched by the large amount of moisture from them, rainfall farther inland, even in the prairie states, would be far less than it is.

In the same manner Hamberg (1885–1889) argues that the forests of Sweden have an important influence on precipitation in countries to the east, into which prevailing winds blow.

9. EFFECT OF FOREST VEGETATION ON CONSERVATION OF WATER

Precipitation which falls upon the land escapes from it in five ways, namely: through evaporation, transpiration, surface runoff, seepage runoff, and deep seepage. By evaporation is meant that part of the precipitation which returns to the atmosphere in the form of water vapor from soil and water surfaces and from objects upon such surfaces, including vegetation. Transpiration loss is that part of the rainfall which sinks into the soil and is later taken up by vegetation through the roots and given off to the atmosphere in the form of water vapor through the foliage and branches. To transpiration loss may be added, although not strictly a part of it, the comparatively small amount of moisture taken up by vegetation which through chemical change becomes a part of the organic vegetable structure. The surface or superficial runoff is that portion of precipitation which, from time of falling until entering the streams, passes over the surface without percolating into the soil. Seepage runoff is that portion of rainfall which sinks into the earth but later reappears on the surface at lower elevations and, with the surface runoff, passes from the drainage basin in streams. Deep seepage is that part of the rainfall which sinks into the soil and percolates to such depths that it does not later appear on the surface of the drainage basin.

10. Effect of Forest Vegetation on Evaporation

In order that moisture which falls to the earth in the form of rain and snow may be most effective in sustaining vegetation and in feeding streams, as little as possible of it should escape in the form of evapora-

tion. How much of the yearly precipitation of a given region is returned to the atmosphere through evaporation can not be measured accurately. The amount varies greatly with heat and moisture conditions, with wind velocity, physical characteristics of soil, and many other factors as well. In all regions a relatively high percentage of total precipitation is returned to the atmosphere in this way. Vegetation and particularly forests, in checking the velocity of wind at and near the soil surface, in slightly raising relative humidity of the air, in shading the soil, in lowering temperature, and in covering the mineral soil with a mantle of leaves and other litter, retards rapid loss of moisture from mineral soil. Loss of moisture through evaporation from surface soil in the open on a windy day may be five times as great as loss of moisture from forest soil of similar character under protection of a forest cover. Evaporation from snow surfaces in the open may be four times as rapid as from similar surfaces protected by a forest cover. Lippincott (1899) has called attention to the fact that in the eastern portion of the San Bernadino Mountains of California, in a basin of 200 square miles with little or no forest, a snowfall ranging in depth from 2 to 5 feet is so quickly evaporated by the dry winds as to disappear entirely in a few weeks' time without materially increasing the flow of streams or appreciably wetting the soil underneath. At the same time, snows that fall in the western portion of the range, under fairly dense coniferous forest, remain much longer and on melting fill the soil with moisture and increase stream flow.

11. **Evaporation from Tree Crowns.** — Water evaporated from tree crowns includes a part of that intercepted by foliage and the transpiration water. Precipitation intercepted by forests is greatest where the vegetation is in full foliage. A large number of experiments have been conducted in different countries to determine the amount of precipitation intercepted by trees. The results obtained show considerable variation, owing to character of forest as to species, age, and density; character of precipitation, as to kind, amount, and intensity; and velocity and direction of wind. Coniferous forests intercept more precipitation than deciduous forests as shown in the following tables from European observations.

RAINFALL WHICH REACHED THE GROUND IN WELL-STOCKED FORESTS, IN PERCENTAGE OF TOTAL

	Beech forest	Spruce forest	Scotch pine forest	Larch forest
Prussian stations	76	78	73	..
Bavarian stations	78	73	66	..
Swiss stations	90	77	..	85

The amount intercepted is least in a young stand and greatest in a dense, middle-aged one. The following table compiled from Swiss observations indicates the effect of age of stand on interception.

INTERCEPTION OF PRECIPITATION BY TREE CROWNS IN BEECH STANDS OF VARIOUS AGES

	Age of stand			
	20 years	50 years	60 years	90 years
	Percent	*Percent*	*Percent*	*Percent*
Proportion which reached the ground	98	73	77	83
Proportion retained by the tree crowns	2	27	23	17

When precipitation is well distributed over the year, fully stocked, mature stands on the average intercept from 20 to 35 percent of the precipitation.

The precipitation intercepted by the crowns of trees is returned to the air through evaporation or else runs down the branches to the boles of the trees and thence to the ground. A considerable part of the intercepted precipitation finally reaches the ground in this way.

The interception of snow by tree crowns is quite different from that of rain. It is much greater in coniferous forests than in deciduous forests, often 4 or 5 times as great. Although fully as large a proportion of winter precipitation may be withheld in the form of snow as of rain, less is returned to the air through evaporation, and more finally reaches the soil by being blown from the branches. On the whole, the average depth of snow in forests is greater than in the open.

In a comprehensive study of rainfall interception Horton (1919) analyzed the numerical factors for calculating interception losses and,

from existing experimental data and from his own researches, developed methods for calculating such losses.

Zon (1927) reports an interesting series of studies made near Moscow which show that the species, density, and age of stand have great influence on amount of snow which reaches the ground under forest cover, as shown in the following table.

INTERCEPTIVE INFLUENCE OF FORESTS ON SNOWFALL

	No. of areas examined	No. of measurements of snow depth	No. of snow samples weighed	Depth of snow			Water equivalent of snow-depth
				Minimum	Maximum	Average	
				Inches	*Inches*	*Inches*	*Inches*
1. Young plantations (2 to 4 years old) and small clearings within the forest......	20	259	7	15.4	26.8	21.9	5.1
2. Birch forest (35 to 75 years old)...................	11	377	27	18.9	26.8	22.2	5.0
3. Oak forest (25 and 90 years old)...................	2	63	3	19.7	27.2	23.5	5.6
4. Pine forest................	32	887	56	11.4	19.7	15.5	3.1
Young (25 to 35 years old).	25	662	43	11.4	19.7	15.2	3.1
Old (60 to 90 years old).....	7	225	13	11.8	19.3	16.4	3.2
5. Spruce forest (25 to 35 years old)....................	21	460	29	6.7	13.8	9.7	2.1
6. Pine forest with admixture of birch (65 to 75 years old)..	4	6	3	14.2	22.8	20.0	4.4
Pine forest with admixture of larch (25 to 35 years old)...	3	74	2	11.4	16.5	15.2	3.1
Pine forest with admixture of spruce (35 years old)......	5	157	9	8.7	15.7	12.9	2.9
7. Spruce forest with admixture of larch................	3	57	2	8.3	21.7	14.1	3.1
8. Cultivated field............	1	332	8	5.1	22.4	13.0	3.1

12. **Evaporation from the Ground.** — Evaporation is considerably less from forest soil than from soil in the open. It is also less from a free water surface in a forest than it is from a similar surface in the open. Numerous observations on evaporation from both water and soil inside forests and in the open have been made in Germany, Austria, France, and Russia. These observations show that evaporation from a free water surface in the open is from $1\frac{1}{2}$ to $2\frac{1}{2}$ times as great as in the forest. The Bavarian and Prussian observations show the following annual losses:

Stations	Quantity of water evaporated from a free water surface, depth in inches			Less in forest expressed in percentage of total quantity evaporated in the open
	In the open	In forest	Less in forest	
Bavarian....	23.53	8.61	−14.92	−63
Prussian.....	13.16	5.98	− 7.18	−55
Mean.....	18.34	7.29	−11.05	−60

Observations to determine the effect of forests on evaporation from the soil are less conclusive, owing to the greater difficulty in developing methods for accurate observations. When soil is kept at the point of saturation, Ebermayer (1873) found that the average summer evaporation from forest soil without a covering of leaf litter was 39 percent and with a covering of leaf litter but 15.4 percent of the amount evaporated from a similar soil in the open. Ney (1894) found the evaporation from soil in a beech forest with undisturbed litter to be but 6 percent of the precipitation, and without litter, 15 percent. He found evaporation from soil in a pine forest with leaf litter to be 15 percent and without leaf litter 24 percent of the precipitation.

The decreased evaporation from saturated soil and from free water surfaces in forests is due to the following:

1. Lower wind velocity.
2. Decrease in air and soil temperature.
3. Greater relative humidity.
4. The litter and other cover over the mineral soil.

Wind, by constantly changing air in contact with the soil or other moist surface, has a great influence on evaporation. Other factors being equal, the higher the wind velocity the greater the evaporation. Forest cover by breaking the force of wind at or near the ground reduces evaporation from forest soil. The effect of forest in reducing evaporation extends for considerable distance to the leeward of the trees (King, 1894). Bates (1911) has shown that the effect of windbreaks composed of trees is to reduce evaporation from the soil over an area to the leeward 12 times as wide as the height of the trees, of from 11 to 40 percent, depending upon wind velocity.

The effect of forest litter in reducing evaporation from the ground is shown by researches in Bavaria. Observations extending over a period of 5 years show that forest litter on the average reduces evaporation from soil by 24 percent.

13. Effect of Forest Vegetation on Transpiration Loss

A large part of the water absorbed by vegetation is taken from the soil, enters the transpiration current, and is returned to the air through the leaves. This may be termed physiological evaporation as it is essential for the life processes of trees. Loss of moisture from the ground through transpiration is very large in well-forested regions and nothing on barren soil. Although extensive experiments have been undertaken in many localities in an effort to determine the amount of transpiration water lost from different kinds of vegetation and from different species of trees, the problem is so complex that as yet but little dependable information is available.

In this connection, the following table by Höhnel (1884) is of particular interest as it indicates the consumption of water by different trees, during the growing season.

AMOUNT OF WATER TRANSPIRED BY DIFFERENT FOREST TREES PER POUND OF DRY LEAF SUBSTANCE

	1878	1879	1880
	Pounds	*Pounds*	*Pounds*
Birch	679.9	845.1	918.0
Ash	566.9	983.0	1018.5
Hornbeam	562.5	759.0	871.7
Beech	472.5	859.5	913.8
Maple (Spitzahorn)	462.9	517.2	611.8
Maple (Bergahorn)	435.8	618.3	703.8
Elm	407.3	755.0	822.8
Oak	283.4	622.2	691.5
Oak (Zerreiche)	253.3	614.2	492.2
Spruce	58.5	206.4	140.2
Scotch pine	58.0	103.7	121.0
Fir	44.0	77.5	93.8
Austrian pine	32.1	99.9	70.0

Ney's (1901) computations show that the total amount of water transpired by a fully stocked beech forest during the growing season is equivalent to 10.8 inches, spruce 8.3 inches, and Scotch pine 2.9 inches over the entire area.

The above data indicate a very large consumption of water by forests, much more than by most other forms of vegetation. This is also shown by the fact that forests often lower the water level in a soil and that the layers of forest soil below the surface are usually drier during the grow-

ing season than layers at the same depth in the open. Although evaporation from soil is much less in a forest, the loss from evaporation and transpiration combined may be and usually is much greater than from denuded areas.

Höhnel concludes that a fully stocked mature stand of beech consumes annually as much as 2,140 tons of water per acre. Expressing the amounts of water that were consumed in 1880 in percentage of precipitation of that year, he found that elm transpired 43.5 percent and beech 25 percent of the precipitation.

Research extending over a period of 2 years in the Yale Forest near Keene, New Hampshire, showed that a denuded, coarse, sandy soil, or even a grass-covered soil, in the open is much more moist during the growing season than a similar soil bearing a fully stocked stand of 60-year-old white pine (Craib, 1929). In general, forest soil, mainly because it contains more organic matter and has a lower volume weight, has a higher water content per unit of volume in winter and early spring than similar soil in the open. In May or early June, however, owing to the large amount of water required to supply the transpiration current in a forest, there is a rapid decrease in soil moisture, and from this time forward, during the remainder of the growing season, there is much less water in forest soil than in a similar soil in the open. The large consumption of water by a fully stocked stand of white pine can be demonstrated by trenching around a quadrat beneath the canopy in a mature pine stand. At critical periods of drought during the growing season, there is 2 to 9 times as much available water in the soil in the trenched quadrat at depths down to 3 feet as in similar but untrenched quadrats.

14. Effect of Forest Vegetation on Surface Runoff

The relative amounts of the two classes of runoff, surface and seepage, can not be determined separately. The total runoff, however, can be measured with a fair degree of accuracy. Surface runoff is floodwater often of destructive significance, whereas seepage runoff gives streams their sustained flow and is of great constructive significance. It is, therefore, very easy to see that any factor which decreases surface runoff, and as a consequence, increases seepage, is of utmost economic importance in the utilization and conservation of water.

The relative proportion of surface runoff to seepage is determined by a large number of variable factors of which the forest is one of great importance and the only one entirely under the control of man. The most important of these variable factors are:

1. Amount and character of precipitation.
2. Character of topography.
3. Character of soil, parent material, and geologic substratum.
4. Character of vegetation.

It is mainly these four factors that determine what proportion of the rainfall will escape as floodwater. These factors determine what portion of precipitation will be absorbed by the soil and become the greatest of all factors in promoting forest growth.

It is well known from direct observation that a slowly falling, prolonged rain, even on bare soil on steep slopes, is practically all taken up by the soil. On the other hand, a heavy shower of equal amount but of short duration may largely be lost as surface runoff. The effect of a dense forest canopy is to prolong very materially the time over which precipitation reaches the soil. This is clearly evident in the fact that water will continue to drip from the foliage for an hour or longer after a heavy shower. Therefore, by extending the time over which precipitation reaches the ground, a forest lessens surface runoff.

The rapidity with which precipitation is absorbed by soil is determined largely by the physical condition of the mineral soil, its humus content, and the character of the overlying litter. Forest soil on the whole absorbs water more rapidly than most other soils. In every forest where leaves and other organic débris form a thick covering over the mineral soil, there is practically no superficial runoff except on steep slopes; but when the organic material has been removed by fire or other causes, surface runoff is excessive, as shown by rapid and deep erosion.

Researches by Burger (1923) show a remarkable contrast in the time required for a given volume of water to pass from the surface into a forest soil, as compared with a similar soil in the open. He found that forest soil beneath normal litter has numerous burrows formed by animals and various openings due to decayed roots. There are none of these burrows and other openings from the surface downward in soil in the open. At times of heavy precipitation the rapid seepage of water into forest soils is largely due to these openings. Burger found that the time required for a given volume of water to sink into forest soil over a unit of area was often less than one-fifth the time required to sink into similar soil in the open, and the more compact and the finer the soil texture the greater the difference in time required. Similar studies made at Keene, New Hampshire, by Craib (1929) corroborate the above results.

The rapidity of absorption depends largely upon the length of time precipitation remains available for absorption where it falls or, in other

words, upon the rapidity of surface flow. The longer the surface flow is in reaching streams, the greater will be the amount taken up by a soil. The rapidity with which the surface flow reaches the water courses is determined primarily by two factors:

1. Topography of the region, that is, degree of slope over which the water flows.
2. Obstructions which it meets in its pathway.

When rain falls upon barren soil, moving water, by eroding channels, tends to form small rivulets and then larger ones which flow with a constantly increasing velocity. As a result, the water on the surface passes rapidly over the soil to streams and only a minimum amount penetrates the soil. When the surface soil is covered with various obstructions such as those offered by a forest with its accumulation of litter and plant growth, living and dead, rainfall which is not immediately absorbed at the point of falling is checked in its flow over the surface, and consequently there is more opportunity for it to enter the soil.

The actual amount of surface runoff, particularly at periods of excessive precipitation, is determined not only by rapidity of absorption and slowness of surface flow, but also by the structure and depth of soil and soil cover which is capable of absorbing precipitation and retaining it (Meginnis, 1935).

Forests have great influence on the amount of the absorbing medium in mountainous regions, because of:

1. The large amount of decaying organic matter which it provides and the absorptive capacity of moss and other plant materials which occur in forests.
2. The greater depth of soil resulting from the effects of forests checking wind and water erosion and the effect of vegetation in decomposing underlying rocks.
3. The more broken condition of underlying rocks through the action of deep-rooted plants, more particularly forest trees. Such plants send down their roots into narrow rock fissures, by their growth widen the fissures, and by their death leave openings into which water passes.

15. Effect of Forest Vegetation on Seepage and Water Retention

Forest vegetation, by reducing surface runoff, increases the amount of water that percolates into a soil. The effect of forests in preventing freezing of forest soil is of vast importance in increasing the amount of water that percolates into it, particularly during the spring months. How much precipitation percolates into the soil depends largely upon the volume of soil and its character (Auten, 1933). When soil becomes saturated with water, and precipitation continues, the

effect of a forest ceases, because the water, no longer held back, finds its way into water courses as rapidly as it falls. If the soil is shallow, it can hold back but a comparatively small amount of precipitation. Forest cover, in increasing the volume of soil in mountainous regions over the solid rock foundation, increases seepage. The living and non-living vegetation peculiar to forests absorbs vast quantities of water in proportion to its volume or weight. Thus, species of *Hypnum,* which grow under the shade of trees, absorb 5 times their weight of water; whereas various mosses in the genus *Sphagnum* absorb 10 or more times their weight of water. The humus layers, characteristic of every well-managed forest, absorb from 2 to 4 times their weight of water. Forest soil with its overlying organic layers is in a real sense a vast sponge capable of absorbing much more water per unit of area than soil in the open. After a prolonged summer drought forest soils in the mountains of southern California are capable of absorbing from 15 to 18 inches of rainfall before the streams appreciably increase their flow.

Forest litter not only reduces surface runoff, particularly from finer-textured soils, but this influence continues long after the litter is completely saturated (Lowdermilk, 1930, 1933, 1934). Destruction of forest litter, and the consequent exposure of soil, greatly decreases the absorption rate of soil. Suspended soil particles in runoff water from bare soils are filtered out at the surface and seal the pores and seepage openings sufficiently to account primarily for marked differences in rate of absorption between bare and litter-covered soils. The capacity of forest litter to absorb rainfall is insignificant in comparison with its ability to maintain maximum percolating capacity of soils for precipitation waters.

16. Effect of Forest Vegetation on Springs

Part of the water that seeps into soil at higher elevations reappears at the surface lower down in springs. A forest through its influence in increasing seepage and decreasing surface runoff provides a larger supply of ground water, particularly in mountainous and hilly regions, for the feeding of springs. Not only is the volume of flow from springs in mountain forests greater but it is much more uniform than in denuded regions which are otherwise similar. This is due to the permeability of the forest soil and the depth to which water percolates before it reappears in springs. In mountain regions springs usually diminish their flow and exhibit greater fluctuations in flow with the removal of a forest. In level countries where the general effect of a forest is to drain the soil and lower the ground water, springs seldom occur and the effect of the forest upon them is of minor importance.

Vermeule (1900) from studies made in New Jersey has reported the amount of water, expressed in inches of rainfall, that reaches streams through springs and by underground seepage from forested, cultivated, and denuded watersheds during the dry season when rainfall equals evaporation and its effect on stream flow is eliminated.

YIELD OF SPRINGS ON FORESTED, CULTIVATED, AND BARREN WATERSHEDS DURING DROUGHT

Month	Forested watershed, Passaic	Cultivated watershed, Raritan	Barren watershed
	Inches of rainfall	*Inches of rainfall*	*Inches of rainfall*
First	1.16	1.43	0.94
Second	.54	.64	.38
Third	.40	.45	.26
Fourth	.33	.35	.20
Fifth	.32	.30	.14
Sixth	.31	.27	.12
Seventh	.30	.25	.10
Eighth	.29	.23	.08
Ninth	.28	.22	.07
Total	3.93	4.14	2.29

Writings on forest influences abound in authentic records of the disappearance of springs after destruction of forests in mountainous regions, particularly in regions where rainfall is scarcely adequate for vigorous forest vegetation. Numerous cases have been cited where springs dried up or noticeably decreased their flow after deforestation. In some instances springs reappeared after reforestation.

During a period of 22 years, 9,507 wells in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Ohio, Tennessee, and Wisconsin showed a lowering of the ground water at a minimum mean rate of 1.32 feet in the 80 years since settlement began (McGee, 1911). This lowering of the ground water is probably due to increased surface runoff and decreased seepage following the progressive removal of forests.

17. Effect of Forest Vegetation on Stream Flow

Stream flow includes that part of precipitation which remains after the loss through interception, evaporation, transpiration, and the small amount which percolates to such depths that it does not reappear on the surface of a drainage area. Stream flow includes surface runoff, or floodwater, and seepage runoff, or that which reaches streams after

percolating through the soil. The relative proportion of surface runoff and seepage runoff in streams depends primarily upon topography. For this reason the effect of forests on stream flow is different in level countries from what it is in mountainous regions. In level country surface runoff comprises a comparatively small part of precipitation. On the other hand, in mountainous regions denuded of vegetation, it may equal 80 percent of the annual precipitation.

The following table compiled by Zon (1927) shows the annual loss of precipitation by interception, evaporation, and transpiration in flat country:

LOSS OF WATER TO STREAMS IN FORESTS IN FLAT COUNTRY (ANNUAL PRECIPITATION 31.5 INCHES)

	Interception by forest cover	Evaporation from soil	Transpiration	Total loss	Loss of annual rainfall in percentage of total
	Inches	*Inches*	*Inches*	*Inches*	
With leaf litter:					
Beech	6.7	1.9	10.8	19.4	61.5
Pine	9.4	2.8	3.1	15.3	48.6
Spruce	12.1	2.6	9.1	23.8	75.6
Average	9.4	2.4	7.7	19.5	61.9
Without leaf litter:					
Beech	4.7	4.7	10.8	20.2	64.1
Pine	6.3	7.6	3.1	17.0	54.0
Spruce	10.5	6.1	9.1	25.7	81.6
Average	7.2	6.1	7.7	21.0	66.7

The amount of water available for stream flow in flat country covered with dense forest vegetation is less than in flat country denuded of vegetation, directly because of the large consumption in supplying the transpiration current. Although much depends on the particular conditions of climate and soil, in level regions where there is no surface runoff ground water is usually lower in a forest than outside, this condition being particularly noticeable in regions of deficient rainfall.

In mountainous regions where the larger percentage of stream flow is surface runoff, the influence of forest vegetation in reducing surface runoff and increasing seepage is of vast and far-reaching im-

portance. Ney (1894) estimated that the amount of water that forest vegetation saves to German soil in mountainous regions, by converting surface runoff to seepage, is approximately 50 percent of the precipitation. Measurements taken in France show that the surface runoff from forested slopes is only about one-half as much as from deforested slopes, whereas on hilly land covered with dense stands of timber and with abundant leaf litter the surface runoff is little or nothing. In order that a forest may have its maximum effect in reducing surface runoff the soil should be covered with an unbroken leaf litter. It should not be burned over or grazed.

The rapidity of the stream flow, as influenced by forest cover, is clearly shown in a comparison of timbered catchment areas with non-timbered areas. On well-timbered catchment areas the maximum stream flow does not occur for some time, often several hours after precipitation ceases, and its subsequent decrease is gradual from day to day. On non-forested catchment areas, on the other hand, and particularly small ones, maximum stream flow may occur within an hour or two after maximum rainfall, and after precipitation ceases the decrease in stream flow is very rapid.

Two serious attempts have been made to measure the influence of forests upon stream flow. Engler (1919) reports the results of 15 years of observation near Emmental, Switzerland, which are largely qualitative because stream-flow relationships under similar conditions of cover were not established. Bates and Henry (1928) give the results of 15 years of study of two watersheds in the Rio Grande National Forest, near Wagon Wheel Gap, Colorado. Observations on the two forested watersheds were continued for 8 years to afford comparisons before deforestation. One watershed was then denuded and records were continued for 7 years more to bring out the effects of deforestation. Excess stream flow from the denuded watershed averaged about 0.96 inch of stream discharge[1] for the 7 years after denudation. The greatest excess occurred during the third year and amounted to nearly 2 inches, whereas in the sixth and seventh years it had dwindled to a little more than one-half inch because of the progress of natural revegetation of this watershed. The greater portion of the excess discharge resulting from denudation occurred in the spring flood and in the earlier part of that flood. Bates and Henry (1928) propose that the ratio of

[1] Thus 1 inch of stream discharge implies that the watershed of a stream supplies an average of one-twelfth acre-foot of water for each acre of the entire watershed, although individually some acres actually supply more and others less than this amount.

high to low stages in stream flow indicates the liability of failure of a watershed to exercise its full storage function and hence the need for protective influences which will cause that function to be exercised to the fullest possible extent, with the probability that so far as spring storage of water is increased summer flow will be increased, and will not be appreciably decreased by the growing-season drain of the forest cover.

The reduction of surface runoff not only increases seepage but it also prevents erosion. Both of these are factors of importance in the conservation of water for power and for human consumption. Steadiness in the flow of stream is largely a question of the proportion of surface runoff to seepage runoff in the discharge. For this reason the fluctuations in discharge in mountainous regions are much greater than in flat regions. When regions having rough topography are denuded, the percentage of precipitation that escapes from a drainage area in streams is inordinately high, sometimes as much as 80 percent more. Nearly all, however, escapes as floodwater during or following storms. Seepage runoff is so small that the streams are dry, or nearly so, for a great part of the year.

Although a forest may use more water during the growing season than it receives in precipitation, it stores much more in the soil during the so-called dormant season. It forms a reservoir which is filled with the excess water when flood danger is greatest and is slowly given out to vegetation and to sustain stream flow at times of drought. Forests, especially of conifers, may materially delay snow melting and thus not only result in more water being added to the soil, but may also retard the occurrence of early summer droughts (Carpenter, 1901; Betts, 1916; Griffin, 1918; Bates and Henry, 1928).

18. Effect of Forest Vegetation on Floods

Floods causing overflow of rivers can be directly traced to very heavy and long-continued rains, or to rains combined with rapid melting of snow. Forests, in reducing surface runoff and increasing seepage, extend the time over which precipitation reaches streams. As a result, a flood is slower in rising and the crest is not so high. The most striking influence of forest vegetation on stream flow is shown where heavy rainfall follows a long period of dry weather in mountainous regions. When heavy downpours occur at such times forest soil, owing to its larger volume and greater absorptive capacity, is capable of taking up and holding much more water than denuded soils that are otherwise similar (Zon, 1927; Shepard, 1928; Sherman et al, 1929; Bailey, Forsling, and Becraft, 1934; Meginnis, 1935; Munns and Sims, 1936). Observations in the San Bernadino mountains in California

show that a November rainfall of 20 inches, when preceded by several months without precipitation, is all absorbed by forest soil and streams are not materially increased in flow (Toumey, 1903). On the other hand, a later rainfall of 5 inches, after the ground is thoroughly saturated, practically all appears in the discharge of streams on the drainage area. After the ground is once saturated a forest has little influence upon the floodwater until it dries out again. Mead (1911) in his study of Wisconsin streams states that a rainfall of 3 inches or more per month during the spring gives rise to a stream flow of large magnitude, but the same amount of precipitation during the later summer and early autumn has little or no effect in increasing discharge of streams. In general it may be said that the amount of water carried by a stream during the year on a given watershed depends upon the amount of precipitation. The amount carried during different seasons of the year, however, depends upon the storage capacity of the watershed or what proportion of the total precipitation reaches the streams as soon as it falls and how much reaches them through seepage after precipitation ceases.

Although climate, soil, topography, and meteorological conditions play the most important part in causing floods, deforestation must also be considered an important factor and one which is under the control of man (Fernow, 1890). Although forests can not be depended upon entirely to prevent the occurrence of our highest and most destructive floods, they aid materially by rendering the flow throughout the year more uniform, thus making the low stages of stream flow higher and the high stages lower. Floods can be controlled effectively only under a coordinated program of rational land management, soil conservation, reforestation, and upstream engineering on the headwaters, together with downstream engineering works on the larger rivers.

19. EFFECT OF FOREST VEGETATION ON AIR CURRENTS

As forests break or moderate the force of air currents they serve to protect lands lying to their lee against cold and dry winds and against winds of high velocity. This influence of forests may be beneficial or detrimental, depending upon locality and season of the year. The term windbreak is applied to any object which serves to obstruct the free movement of surface winds. So far as it relates to vegetation, windbreaks may be divided into three classes:

1. Hedgerows.
2. Shelterbelts.
3. Groves and forests.

Trees are extensively used to check the movement of drifting sand, and to protect fields, orchards, nurseries, buildings, and livestock. As destructive winds in different regions come from different directions, windbreaks are located entirely with reference to the direction from which the winds come.

20. How Windbreaks Act

A windbreak affects the adjacent fields and buildings only through its effect on the atmosphere and soil. In other words, it affords protection by deflecting air currents, thus modifying their effect on the soil and air. The effect of a windbreak on an adjacent open area is both beneficial and detrimental. It is usually detrimental to the land that borders the windbreak because of competition of the windbreak with the lesser vegetation for soil moisture and nutrients. Immediately beyond the zone where the lesser vegetation competes with the windbreak the influence of the windbreak is for good, as it reduces velocity of the wind, thus lessening evaporation, which is always increased by air currents. By stagnating the air it increases the extremes of temperature in both air and soil and causes changes in distribution of atmospheric moisture. In general, other things being equal, the influence of a windbreak on areas adjacent to it is proportional to its height. The damage to the vegetation at the sides of the windbreak extends over approximately the same area as is occupied by the tree roots, which may roughly be considered as that of the shadows thrown by the windbreak at mid-day during the growing season.

In plains regions the beneficial effects of windbreaks and shelterbelts generally far outweigh their injurious effects. The main beneficial effects of shelterbelt planting result in amelioration of environmental conditions, particularly the chain of physical effects resulting from retardation of surface wind movement (Silcox et al., 1935). Evaporation from the soil immediately adjoining a shelterbelt is reduced. Transpiration from vegetation is retarded. Drifting of snow is checked, and blowing of soil is lessened.

21. Effect of Windbreaks on Air and Soil Moisture. — The greatest influence of a windbreak, and the one which, on the whole, is of greatest benefit, is its effect upon moisture conditions, because of decreased wind velocity. Adjacent to a windbreak the soil is sapped of its moisture by the trees, and, as a consequence, there is less available soil moisture for the vegetation. In this respect, therefore, the windbreak is harmful. Usually, however, the competition for soil moisture does not extend much beyond the spread of the crowns. The harmful

effect of competition for soil moisture adjacent to a windbreak can be remedied by thorough and deep cultivation of soil adjacent to the windbreak, by subsoiling or dynamiting the subsoil before planting the windbreak in order to encourage deep rooting, or by planting only deep-rooted species. Beyond the zone of competition and within the area of windbreak protection a windbreak exercises a beneficial effect on vegetation in all regions deficient in available soil moisture. The effect of windbreaks in reducing evaporation has been demonstrated by King (1894), Card (1897), and Bates (1911).

The effect of windbreaks on air and soil moisture is measured by differences in evaporation within the area influenced by the windbreak as compared with similar areas outside. Evaporation records on areas influenced by a great variety of windbreaks and under different conditions of temperature and wind velocities, led Bates (1911) to the following conclusions:

1. The efficiency of a windbreak in checking evaporation is proportional to its density. In extreme cases it may save at a single point 70 percent of the moisture ordinarily lost by evaporation.

2. The area protected is proportional to the height and density of a windbreak, and the distance to which its protection is felt increases with wind velocity. Protection is appreciable to the windward for a distance equal to 5 times the height of a windbreak and to the leeward for a distance of 15 to 20 times the height.

3. The distance from a windbreak of the area of greatest protection depends upon the position of the mass of foliage which affords the protection; in a dense grove it is immediately in the lee of the trees; in a single line of trees or a narrow belt without lower branches it may be as much as 5 times their height. Furthermore, the area of greatest protection moves toward the windbreak and away from it with a change in the velocity of the wind.

4. If a windbreak is dense enough to resist the strongest wind, the protection which it gives to any point in its lee increases with an increase in the wind velocity. In a moderately dense windbreak, the efficiency remains about the same under all conditions, because leakage through the windbreak is about proportional to the total amount of wind. With a very open windbreak, the efficiency decreases with a decrease in wind velocity. As a specific illustration of the effect of a good windbreak in reducing evaporation from an adjacent field protected by it, a windbreak 100 feet high and half a mile long will reduce the evaporation from 73 acres by 32 percent where the mean wind velocity is 10 miles per hour.

22. Effect of Windbreaks on Temperature. — A well-developed windbreak affects to a marked extent air temperature within the zone of its influence. From the influence of windbreaks on air temperature the following conclusions may be drawn:

1. Other conditions being equal, both the highest maximum temperature at mid-day and the lowest minimum temperature at night are found at the same

point relative to a windbreak and exceed about equally the maximum and minimum temperatures in the open.

2. In the zone of windbreak influence, the highest temperatures on clear, sunny days and the lowest temperatures on clear, cool nights occur at the points of greatest windbreak efficiency, that is, the point of greatest air stagnation.

3. After several days of cloudiness the windbreak has no further effect upon air temperature.

Within the area of influence that is constantly shaded by the windbreak the soil temperature is considerably cooler than beyond the area of influence. Outside the area of constant shading, however, the soil temperature is higher. The above applies only during the period of seasonal increase in temperature. When the seasonal decrease in temperature begins in late summer or autumn and more heat is radiated from the ground than it receives, the relation of temperatures within the area of influence and outside of it is reversed.

23. EFFECT OF FOREST VEGETATION ON AVALANCHES

Forests not only have a beneficial influence on the conservation of snow (Church, 1912, 1913), but they also are an important factor in preventing damage by avalanches in alpine regions. In Switzerland and other mountainous countries, protection forests are sometimes carefully developed and maintained in order to safeguard the lower lying country from damage by moving snow and ice. For many years it has been the special aim of the Swiss government to extend the limit of tree growth as high on mountain slopes as possible in order to prevent the formation of avalanches which occur where slopes are bare. When the places where avalanches originate are so high that tree growth is impossible, terraces, ditches, posts, and other obstructions are placed at the points where avalanches begin to form in order to keep the snow from slipping.

24. Kinds of Avalanches

Avalanches are of various kinds, depending upon character and condition of the snow and ice of which they are composed. Always, however, they are masses of snow and ice, which, becoming dislodged from the place of origin on the upper slopes of a mountainside, slide or fall into the country below. They cause so vast an amount of damage in localities where they are of frequent occurrence that protective measures are essential. In general, avalanches may be classed under the following heads:

1. Dust avalanches.
2. Glacier avalanches.
3. Ground avalanches.
4. Top avalanches.

These different types of avalanches differ in a number of respects. *Dust avalanches* are composed of very fine snow which fills the air with a dense cloud of minute particles as they proceed along their course. They usually arise far above timberline during very cold weather. *Glacier avalanches* are composed of masses of compact snow and ice which break from the upper margins of precipitous glacial fields, usually during the summer months. *Ground avalanches* are snow fields formed on smooth surfaces, which, under special conditions, slip or slide to lower levels. They usually form at moderate elevations, often below timberline, when a large snowfall has become heavy from rain or from thawing. *Top avalanches* differ from ground avalanches in that they slip or slide over a crust of older snow. The ground and top avalanches, forming as they do at lower elevations, are far more destructive than the others.

25. Relation of Forest Cover to Ground and Top Avalanches

Munger (1911) has shown that ground and top avalanches in the northern Cascades are of two types, namely, the canyon slide and the slope slide, with every intermediate stage between the two. The canyon slide originates on cliffs at the head of a canyon and proceeds down the bed of the canyon as a narrow body of snow increasing in volume as it proceeds. The slope slide originates on a steep slope. It forms when a snow field, often on an entire hillside, breaks loose from the snow mantle above and slowly moves over the slope to lower levels. As the slope slide may involve large areas, the aggregate weight of the moving snow mass gives it great crushing and destructive power.

Canyon slides, originating as they do at the head of steep, rocky canyons, for the most part follow well-worn avalanche slideways, entirely denuded of forest vegetation. As they are of frequent occurrence a forest has no chance to develop and hold the snow in place. Protection against them can be attained only by the erection of artificial barriers.

Although many slope slides occur high up on the mountains above timberline, they are common on denuded areas, well below timberline. They are not infrequent on areas that have been denuded in recent years and where they did not occur when the forest cover was intact. Here they are occurring, not because the slopes are precipitous but because the protective forest covor has been removed.

Preventive measures against damage from avalanches can be attained either by erecting artificial barriers or by reforestation. Artificial barriers are usually impracticable in the United States because of the expense involved. Reforestation is often possible and practicable. As pointed out by Munger (1911), avalanches of the slope-slide type are unnecessary and preventable. Their frequency can be lessened by adhering to the following principles:

1. Proper care of forested areas in localities where avalanches are likely to occur. This care centers in fire protection.
2. Exclusion of grazing, particularly by sheep and goats.
3. Reforestation of all denuded areas. When protection from fire will not be followed by natural regeneration, artificial means must be employed.
4. Cutting of timber by a selective or partial-cutting method. Continuity of the forest cover must be kept unbroken.

26. EFFECT OF FOREST VEGETATION ON SOIL

The beneficial influence of forest vegetation on soil is due to its mechanical effect and its power of increasing fertility of the land by adding nutrients. The mechanical effect of a forest on soil makes itself felt chiefly in preventing the transportation of soil from its place of origin to lower altitudes. By so doing it becomes the chief factor in determining depth of soil on mountains, hills, and sloping ground, in binding shifting sand, and in preventing wind and water erosion. By improving fertility of soil a less exacting species may be useful in bringing the soil into condition for successful growth of a more exacting species. Were it not for this beneficial effect of vegetation on soil fertility, succession in the development of forest vegetation would be impossible. In succession, one kind of vegetation prepares the way for a more exacting kind until finally the climax type for the particular site is developed.

In general the influence of forest vegetation on soil relates to the producing of a new substratum of soil and the changing of soil structure. Forest vegetation assists in the formation of soil by the accumulation of plant remains, by stimulating weathering through the action of acids formed by vegetation, and by the resistance which forest vegetation offers to moving air and water. Forests modify soil structure primarily through the addition of organic matter following death and decomposition of leaves and other plant parts and through root penetration and animal activity.

27. Effect of Forest Vegetation on Wind Erosion

Soil is transported from one place to another either by wind or by water. Forests, by checking the velocity of wind and by reducing sur-

face runoff, have a great influence on the stability of soils. Exposed soils, without sufficient clay or humus for binding materials, are often blown about by wind, the degree of instability depending upon wind velocity. Sands subject to wind erosion should be covered with forest growth or other soil-binding plants because permanent stability can be attained only where sands liable to shift are so covered (Kellogg, 1915).

When, for one reason or another, soils subject to movement by the wind become denuded it is essential that they be covered with forest vegetation as soon as possible. In some instances this may necessitate the construction of mechanical barriers and the planting of beach grass or other lesser vegetation before the forest can be reestablished (Gerhart, 1900). The action of beach grass and other pioneer grasses in causing the dropping and stabilization of wind-blown dust and sand, produces stable centers for the invasion of other plants. With the increase in individuals and particularly invasion by trees, the amount of organic matter increases. The soil becomes more retentive of water and contains more nutrients.

28. Effect of Forest Cover on Water Erosion

One of the most important and far-reaching influences of forests is the protecting of the soil from erosion (Ashe, 1926; Bennett and Chapline, 1928; Meginnis, 1935; Renner, 1936). The control of erosion is of particular importance in land management in all regions having well-marked topographic relief. The effect of forest vegetation upon material carried by water is in reducing velocity of the current and causing the deposition of its load in whole or in part. The removal of the material when once deposited is made difficult by plant remains and particularly by roots. The extent to which soil suffers from erosion is for the most part determined by the following factors:

1. Climatic conditions.
2. Geological formation.
3. Character of soil.
4. Steepness of slope.
5. Character of surface.

Regions having steep slopes and weak, underlying rocks, and a surface bare of vegetation and subject to torrential rains, suffer most from erosion. In such regions surface runoff reaches vast proportions and carries the largest amount of silt, sand, and other débris. On the other hand, regions with a dense, unbroken forest vegetation, even where slopes are steep and the underlying rocks weak, have but little erosion. The damage from erosion is not only in the locality where

erosion occurs, but it is also in valleys and streambeds. Débris eroded from higher elevations, when deposited in streambeds, obstructs navigation. Glenn (1911) directly traces the fluctuations in regularity of flow of many streams in the southern Appalachian Mountains to denudation of mountain slopes and erosion resulting therefrom.

The surface soil in mountainous regions is a more or less thin covering over bedrock. It has taken generations to form under the action of rock weathering and through the accumulation of organic matter, the whole being held over the rock foundation by the roots of vegetation and protected by the accumulation of organic matter. When forest vegetation is removed the organic matter disappears, and the thin layer of soil is washed from the slopes, exposing bare rock. This process may convert a previously productive region into a devastated area where it is impossible to bring back forest vegetation without artificial means and the expenditure of large sums of money.

29. Methods of Preventing and Overcoming Damage from Water Erosion. — It is far easier and less expensive to prevent erosion from taking place than it is to check and overcome it after it has once begun. Wherever mountain soil is likely to become unstable when exposed, it should be kept permanently in forest growth. Fires should be eliminated, grazing restricted, and only selective cutting practiced. Of all natural covers, forests are the most efficient in holding soil on mountains. They are most efficient in preventing the slopes from eroding and the beds of streams from filling with débris (Ashe, 1926). Even after erosion has begun it can be reduced, usually by better fire protection, regulation of grazing, and by other operations that have for their object the improvement of forests (Bennett and Chapline, 1928; Renner, 1936).

After erosion has gone so far that a large part of the soil has been washed from the bedrock it becomes extremely difficult to check further erosion by natural means. The reestablishment of forest vegetation is no longer possible without the expenditure of large sums of money for revetment or other engineering works and for artificial regeneration. Before artificial regeneration can be undertaken it is often necessary to build check dams in gullies and obstructions across the beds of streams and their tributaries in order to prevent further streambed erosion. Systems of terraces must be constructed on slopes in order to reduce the gradient and prevent further washing. In extreme cases soil, in which the regeneration is started, is brought back by hand labor (Wang, 1890).

CHAPTER XII

EFFECT OF FORESTS ON ANIMAL LIFE, PARTICULARLY MANKIND

1. EFFECT OF FORESTS ON ANIMAL LIFE

Plants are probably the most important features in the environment of terrestrial animals. All animals are dependent directly or indirectly upon plants for food. Even for carnivores and scavengers that feed upon the bodies of other animals, plants are the original source of food supply of the animals preyed upon, as of all other terrestrial animals. Although animals are not usually restricted to particular plant species for food, they often show a preference for certain general types of food. Plants also provide many animals with shelter from inclement weather, protection from enemies, situations for homes, and materials for nests.

The life of many terrestrial animals is significantly influenced by forests. Many animals are attracted to forests through providing a conveniently sustained supply of palatable food and suitable environments in which to hide, live, and rear their young. Forest animals are therefore likely to develop strong appetites for plant foods found in forests (Dice, 1931).

2. Forests as Source of Food for Animals

Many forest animals feed very largely upon seeds, fruits, buds, leaves, twigs, and other parts of forest plants; others feed in forests when food is plentiful there and scarce elsewhere. From crop examinations of ruffed grouse, Weed and Dearborn (1903) report that the daily requirement of this species is between 800 and 1,000 buds, apple and maple being most often eaten. Miller (1935) reports that apple, poplar (including aspen), and wild cherry comprise more than a third of the winter diet of this bird; acorns make up 5 percent for the entire winter, and the remainder includes fruits of greenbrier, grape, bittersweet, wax-myrtle, winterberry, viburnum, and buds of laurel, willow, maple, and hornbeam.

Although quail may at times feed very largely upon the seeds of herbaceous plants, especially legumes, they are known to eat mulberry fruits, blackberries, redbud, and other tree seeds. Stoddard (1931) reports that in southern Georgia and northern Florida, early in Novem-

ber when pine seeds begin to shower down abundantly, quail coveys that have been feeding in cornfields up to that time move to forested areas. During November, December, January, and February, 32.5 percent of the food of 529 birds examined consisted of pine seeds, 87 percent of birds examined having fed on them. During winters when pine seed is not so abundant covey ranges shift to obtain acorns and seeds of red gum and Florida beggarweed.

Many birds, both migrant and resident, that are ordinarily vegetarians may vary their food habits when insects suddenly become very abundant, as during epidemics. Frequently they are attracted or detained by bountiful supplies of insect food and feed freely upon the most abundant species. Woodpeckers evidently vary their usual diet of ants, beetles, and beetle larvae obtained from dead trees and logs and of seeds of forest trees and shrubs to an extraordinary degree when grasshoppers are very abundant. Birds of prey, as hawks and owls, also feed upon insects when they are abundant. Even pigeons, doves, and other seed-eating birds are known to add a considerable proportion of locusts to their diets during insect epidemics.

Insect pests are responsible for annual losses of forests and forest products which have been variously estimated at 100 to 150 million dollars. The insects causing this damage are, to some degree, held in check by birds. Forests protect birds which, in turn, react on forests. The most valuable tree-protecting birds have decreased very rapidly (Hornaday, 1914). Many of the migratory song birds are now protected by law.

3. Forests as Environments for Animals

The distribution of any species of animal is controlled by the resultant effects of an interaction of all environmental factors. Although many factors are involved in the determination of animal distribution, Dice (1931) regards vegetation as usually most important. Animals are commonly associated with certain types of vegetation in their food requirements, and they are also dependent upon these types for homes and protection rather than upon particular species or taxonomic groups of plants (Silloway, 1923; McAtee, 1926; Cahalane, 1928; Dice, 1931). For example, squirrels, which make their homes in hollow trees during part of each year, are not particular as to what species of tree provides the hollow. Obviously, however, hardwoods supply more suitable nesting places. Eastern gray squirrels are accordingly most commonly found in hardwood forests (Dice, 1931).

The destruction or, oftentimes, even mismanagement of forests cause

valuable game fishes to disappear from small streams and many song and game birds to go elsewhere. Forests provide protection for most terrestrial game birds. Wild turkey, ruffed grouse, and woodcock belong in forests and depend upon them for shelter and food. Various species of deer and many other wild mammals classed as game are more or less dependent upon forests for food and protection. Although deer are not abundant in dense mature forests with scant understory browse, cuttings which favor the establishment of tree reproduction and other palatable browse and the increase of forest " edge " tend to result in an increase of the deer population. Following many years of forest planting on the sandhills in the Nebraska National Forest and the development of forest conditions in the resulting plantations, deer have migrated to the area and are thriving there.

In the transition area lying between the prairie area and the forest belt in the northern part of the north central United States, Leopold (1931) has shown that fire, forest clearing, and cultivation have now added the prairie hen and sharptail grouse to what was originally deer and ruffed grouse range. The northern parts of the forest belt were originally moose and caribou country, but as a result of the northward shift of all species, caused by settlement, the entire belt is now deer and ruffed grouse country. Prairie chickens have successfully invaded the larger cleared and burned areas.

Both composition and density of forest stands may determine the presence or absence of forest animals. Pine plantations are unsuitable for ruffed grouse although natural stands of hardwood are satisfactory. Deer apparently prefer mixed stands of hardwoods and conifers in which the latter are predominant rather than pure stands of conifers. Rabbits are very abundant in dense young pine stands but are uncommon in less dense older pine stands because these usually contain less food and protective cover.

Most species of game animals require from one to four types of environment on each unit of habitable range, and most species require three or four, of which forests provide important types (Leopold, 1933). The maximum production of game animals is attained only where environmental types are so interspersed as to bring each of them within the cruising radius of the species, thus providing vegetative richness and simultaneous availability (Leopold, 1930). Leopold (1933) has developed this concept into his *law of dispersion*, which may be stated as follows: *The potential density of animals of low radius requiring two or more types of environment is, within ordinary limits, proportional to the sum of the type peripheries.*

According to Leopold (1930), deer in the Lake States in summer may require cut-over land for feeding, water for fawning, thickets for hiding, and open land to escape flies, and in winter they may require cedar swamp for yarding. In autumn, oak and beech mast, if not essential, is a decided advantage. Therefore, the tendency of deer is to occupy only such ranges as afford these daily and seasonal needs within their daily and seasonal cruising radii.

A range is habitable for a species when it provides places suitable for the animals to feed, hide, rest, sleep, play, and rear their young, all within a limited cruising radius. Forests afford facilities for some or all such activities by many game animals, which comprise valuable, indirect or secondary forest products in need of protection. Stands of timber and game animals should be so managed that, insofar as possible, each is compatible with the other. Unless forests are managed with this objective, nearly all kinds of game rapidly disappear.

Forests also afford shelter for domestic livestock. Not infrequently the grazing of domestic animals in forests, particularly for a portion of each year, is of far more importance than grazing on open land. The interrelations between forests and grazing animals are often underestimated. They are influenced by the kind of forest, its age and composition, and by climate, topography, and character of locality.

4. EFFECT OF FORESTS ON MANKIND

The inference has already been made that a species of animal (or plant) survives only where and when it encounters an environment which provides adequate means of subsistence for that particular species and which can be endured. Leopold (1933) has shown that the essential difference between deer and man is that man develops and exploits farms, forests, mines, and oil wells, and builds houses, factories, cities, railroads, boats, and airplanes to provide himself with habitable environments, whereas deer must accept the random assortment of environments provided by nature and modified by human action, or go elsewhere. For both that endless competition known as society consists essentially of a struggle for existence and for the best assortment of environments in which to feed, hide, rest, sleep, play, and reproduce.

The life of man and, in fact, of all civilization throughout its development has been profoundly affected by the presence or absence of forests and by the relative abundance or scarcity of forest products.

5. Influence of Forests on Civilization

Forests have had an important influence on the distribution of mankind over the earth's surface. In the early stages of civilization in Europe, Asia, and America forests were unfavorable to settlement by primitive man. Zon (1920) recognizes three stages in the relation of human progress to forests:

1. Civilization dominated by forests.
2. Civilization overcoming forests.
3. Civilization dominating forests.

He shows that just as the stone, bronze, and iron ages existed at the same time on the earth, so also the three stages in the relation of forests to mankind are present simultaneously. In central Africa and parts of Central and South America forests are still dominating civilization; in much of North America and in Asia civilization is overcoming forests; and in Europe and parts of the United States forests are dominated by man.

Forests have greatly influenced the spiritual and religious life of tribes living in or near them. Uncivilized men, because of their nomadic disposition and very simple life of hunting, fishing, and the collection of fruits, barks, and herbs, have for the most part only temporary places of abode. With the advance of civilization, the social development of a people found expression in the concentration of family life in more permanent places of abode; and the development of government resulted in greater security and permanence to homes and domestic life within them and a demand for different building materials.

In regions where forests are abundant, logs and lumber are usually so plentiful and cheap that they are commonly used in the construction of dwellings; but in regions lacking forests or where forest products are scarce or very costly dwellings are built of sod, adobe, brick, or stone.

Wood, in one form or another, is one of the most convenient and necessary commodities used in everyday life of civilized people of the world — in home, office, store, church, or school. Civilized human beings are surrounded from the cradle to the coffin by essential articles made of wood.

6. Sanitary Influence of Forests

Forests, by forming the major part of the vegetation of the earth, are important factors in the production of oxygen through photosynthesis. The former claim of greater oxygen and ozone content of

forest air, however, as emphasized by Ebermayer (1890), does not appear from more recent observations to be of great significance. The much discussed beneficial effects of ozone in forest air seem to lack the support of accepted observations. There are many other ways, however, in which forests have a more or less recognized hygienic significance. These are well recognized by health experts as shown in the location of sanitaria in or near extensive forest areas. There are also very significant hygienic and social reasons for wooded parks and commercial forests near cities and towns. Parks and forests serve as places for healthful relaxation and recreation and where the beauties of nature may be observed, studied, and enjoyed by the people.

The reaction of forests on man, aside from directly or indirectly supplying him with food, shelter, and clothing, is important from the standpoint of hygiene and aesthetics.

The favorable influence of forests on health is chiefly due to the following:

1. Their ameliorating effect upon extreme weather conditions.
2. Their influence on the existence and reduction of pathogenic microbes.
3. Their favorable effect on potable water supplies.
4. Their effect in inducing tranquility of mind.

7. Favorable Effect on Amelioration of Weather

Although the relation of forests to weather conditions is still uncertain, their protective value against most severe extremes of summer heat and winter cold and particularly against daily extremes in temperature is well recognized. This protection, combined with shade and reduced wind movement, makes the weather more comfortable and enjoyable. There are not only advantages from this standpoint for all persons who are ill or convalescent but also for persons in good health (Ward, 1913). Henry (1919) has stressed the sanitary influences of forests because of the protection which they afford in making life more bearable in districts where cold and humid winds prevail. It appears that the action of cold, wet winds on both animals and plants is to reduce vitality.

8. Favorable Effect on Reduction of Pathogenic Microbes

The principal claim for the hygienic significance of forests lies in their influence in reducing pathogenic microbes in the atmosphere because of forest air's being in a condition of relative calm and free from dust. Instances are available where forests are said to have protected the inhabitants against the germs of malaria. In some places a

forest is stated to have the opposite effect, because of the harboring of malaria-carrying insects. Probably the beneficial effect in freeing a region from malaria which a forest exercises is due to lowering of ground water and the effect of this on malaria-carrying organisms. The effect of a forest is to render the height of ground water more uniform. This is closely related to health in country districts which depend upon springs and wells for their potable water supply.

Dust in the air is an important factor in the air's bearing on health. Modern researches show that forest air differs from air over open, settled country not only in respect to its dust content but also in respect to its quality. Extensive studies have been made during the past 50 years on dust in the air. Methods have been devised for counting dust particles in a given volume of air. These particles are many times more abundant over cultivated country than in forests. Dust particles arising from exposed soil and from various industries, and more particularly smoke particles from numerous fires, produce differences observed by the senses in the purity of forest air as compared with the open. As stated by Brewer (1890), the amount and unwholesomeness of dust in the air is intimately related to density of human population. The most harmful ingredients of this dust are:

1. Decaying organic matter.
2. Organisms of all kinds small enough to be carried by the wind.
3. Spores of pathogenic bacteria and fungi.

The air drawn into a man's lungs is equal to 20 to 30 pounds daily. This contains millions of dust particles which adhere to moist surfaces within the lungs. When dust particles are excessive, irritation is set up in an effort to throw them off. When they contain pathogenic germs, disease may ensue.

Investigations carried on for a period of 5 years in France showed that the average number of bacteria in the open in Paris was 3,910 per cubic meter of air and but 455 in the nearby well-wooded parks. In treeless, unpopulated regions, however, such as prairies and deserts, there are no more and often fewer bacteria in the air than in forests.

9. Favorable Effect on Potable Water

A large number of contagious diseases to which mankind is susceptible are carried in water. Microbes which cause these diseases are carried in the surface water into small streams and rivers. It is very important, therefore, that rivers which supply a large part of the potable water of towns and cities come from forested regions. When

potable water is the surface drainage from denuded areas inhabited by man, pathogenic germs which get into the soil are washed into reservoirs and other sources of potable water supply. Filtering such water will not as a rule completely remove such danger. The quality of potable water also depends upon its relative clearness or freedom from silt and other particles which give it a cloudy appearance. Potable water derived from a well-forested watershed has the maximum clearness, and reservoirs remain free from silt. Protection of soil on watersheds from which potable water is derived, by maintaining them in forest, is now recognized as of great importance. Appreciation of this need is shown by municipal water departments and private water companies which are rapidly improving the forest cover on their watersheds.

10. Favorable Effect on Tranquility of Mind

The psychological influences of forests are particularly beneficial to health. To the ancients and people of mediaeval times, forests were places to be avoided. In comparatively recent times, however, there has grown up an absorbing sentimental love of nature, which is a relatively new hygienic factor. It is this which endows forests with a great charm to most of the present generation, making them desirable places for recuperation and the maintenance of health. The usefulness of forests, because of their psychological influence on health, depends upon the character, location, and to some extent, upon the type of forest. Rain forests of tropical countries are depressing and forbidding and are not resorted to for strengthening the feeble and healing the sick. Most mountain forests, however, and particularly coniferous forests of temperate and cold regions, are especially noted for their favorable effects upon invalids.

11. FOREST AESTHETICS

Forests increase the artistic beauty of a country, and consequently they react upon the human inhabitants from an aesthetic standpoint. For a long time an early belief prevailed that dragons and evil spirits were driven from forests but, since about the time that Europe emerged from mediaevalism, such bugaboos no longer have been feared. Forests were thus long held in fear and awe and were seldom if ever made the theme of poet and artist. With the discarding of the mantle of mediaevalism, poets and artists began to see beauty and picturesqueness in forest-clad mountains. With the expansion of the sciences, such as botany and geology, forests became places for study; hence science helped to drive dragons and evil spirits from the forests, and helped to

lead all classes of people to them to admire and love the grand and sublime in nature. The admiration for forests has continued to increase through modern times down to the present and has never been so much a part of our life as it is now.

The original idea of protecting and improving forests and natural parks was for the purpose of building pleasure grounds and not for economic use. Even today this idea is dominant, not only in the treatment of many private woodlands but also in the management of many state and national forests and parks. Thus New York maintains large areas of publicly owned forests primarily for recreational purposes. The sale or use of forest products is prohibited by law. The national government maintains many parks and monuments, varying in area from 2,200,240 acres in the Yellowstone National Park to less than 100 in some of the national monuments. These areas, which include millions of acres in the aggregate, are maintained entirely as pleasure grounds. Grazing is excluded and the mature timber is left uncut. Even national forests are recognized not only as production and protection forests but also as recreation grounds for the nation. This use of the national forests is clearly recognized. The United States Forest Service has established camping grounds, leased sites for hotels and boarding houses, constructed roads and trails, and in many other ways made it possible for the public to use them for recreational purposes.

The love of forests should be fostered and encouraged. It gives a pleasure that can not be perverted, a pleasure that uplifts and never drags down. It is a pleasure which lasts from youth to old age. Fortunately the love of forests is increasing among us. It is a test of true civilization when people abandon more exciting pleasures which often become the source of evil and find enjoyment in forests and mountains. The reaction of forests on man, by increasing the artistic beauty of the landscape, is so far-reaching and profound that it becomes more and more our duty to keep in mind the value of a forest as adornment when we undertake its management for forest products and for protection. This is of particular importance when it is owned by the public and is accessible to large centers of population.

12. Foundations of Forest Aesthetics

Study of the beautiful in the management of forests is necessary if woodland is to serve its highest purpose in its reaction upon the aesthetic side of humanity. There is little doubt but it will receive more attention as a distinct field of forestry, as forest aesthetics becomes better known. Its importance was first made known in 1832 but

emphasis was nowhere placed upon the subject as a study worthy of forest managers until 1883. Since then Salisch (1911) of Austria has been the leading exponent of forest aesthetics as a distinct and worthy branch of forestry. Forest aesthetics considers forest areas which should be managed with a clear conception of beauty. It considers the beauty motive in all operations which are concerned with the production and utilization of forest products on such areas and emphasizes the concept that the motives for forest aesthetics are agreeable and beautiful. Forest aesthetics, in considering the beautiful in nature, points out the relation between the natural and artificial in beauty. The beautiful attractions in forests are considered from the point of view of colors, landscape design, and rock formation. The subject takes under consideration the aesthetic value of different species of indigenous trees, also shrubs and exotics. It considers a forest as composed of plant communities, each varying from the others in structure and in plant forms and consequently expressive of different degrees and kinds of beauty. It considers flowers, and types of foliage, not only of trees but of lesser vegetation on the forest floor. It takes cognizance of natural monuments of the tree world; trees of striking and unusual size and form; sport forms and varieties with variously colored leaves, flowers, fruits, and variously shaped leaves. It also places special emphasis upon worthy historical trees and takes account of the beauty exhibited in the animal life of a forest.

13. Applied Forest Aesthetics

The actual operations concerned with improving forests from an aesthetic standpoint deal with forest vegetation and management and with adornment of forests by conducting operations that make them more beautiful and interesting. Regulation and management from the point of view of aesthetics place special emphasis upon a general scheme of roads, trails, and buildings. It considers the management of species, rotation, reproduction, felling operations, and undergrowth with special reference to developing and enhancing the beautiful and picturesque features. Adornment of forests requires that regulation and management have greater freedom and flexibility. The mode of procedure by which it is to be attained must be a definite part of a management plan. Special attention must be given to beautification of roadsides, to planting in selected places, to the leaving of old trees as landmarks of a forest, to introduction of species, to the appropriate use of stone-work, and to the proper setting of buildings and other structures.

PART III

FORESTS

CHAPTER XIII

FORM AND LIFE OF FOREST TREES

Although silviculturists are chiefly concerned with tree communities and their manner of origin, growth, and development, they are also concerned with the species which make up such communities considered as individuals. They are concerned with trees from a morphological, physiological, and taxonomic standpoint, but more especially in relation to their form, growth, development, and reproduction. In its final analysis, every plant community is composed of a variable number of individual plants. These plants belong to many species, often widely separated taxonomically. They vary in size from unicellular organisms, too small to be observed without a microscope, to large trees. Some are saprophytes living on the decaying organic matter in and on the ground, some are parasites living on trees and other plants; still others are epiphytes and vines for which trees offer mechanical support. Trees of various species, forms, and sizes compete for light, soil moisture, soil nutrients, and growing space; yet among them a great variety of herbs and shrubs find space to grow and develop because they make different demands on a site, particularly for light, moisture, and nutrients. Numerically considered, trees form but a small part of any forest community; the smaller plants far outstrip them in number. Although trees are fewer in number, they form the dominant vegetation in every forest community, give character to it, and are of chief importance to foresters.

1. STRUCTURES AND FUNCTIONS

The part of a tree above ground or the shoot system is composed of the shaft or bole and the crown. The part below ground is the root system. The bole supports the crown progressively rising above the ground and in position for better exposure. The crown spreads out as large an expanse of surface as necessary for the development of leaves, flowers, and fruit. The root system penetrates the soil and extends laterally and occasionally downward in order to give mechanical sup-

port to the parts above ground and supply the tree with water and soil nutrients.

The description of the diverse structural characteristics of the various parts of a tree, such as leaves, buds, twigs, roots, flowers, fruits, and seeds, is foreign to the purpose of this volume and must be sought in works on dendrology. So also the account of the life processes of a tree so far as they relate to the functions of the various plant organs must be sought in works on plant physiology.

2. SPECIES, VARIETIES, RACES, AND INDIVIDUALS

There is not and, from the nature of the case, there can not be absolute uniformity of opinion in the concepts of species, varieties, and races. Each investigator necessarily depends upon the scientific studies that have been made in the past, combined with his own personal work, in determining what individuals he places under given species, varieties, and races. The general conception of species, varieties, and races, as they stand at present, lacks stability, as is clearly shown in the naming of plants. The lack of unformity in the concept necessarily results in lack of uniformity in the naming. A closer approach to uniformity in both respects can be brought about by investigation of the internal structure and physiological characteristics of plants as well as of their external appearance. Mayr (1925) states that differentiation should be based on:

1. External characteristics which together enable one to perceive morphological distinctions (flowers, fruit, bark, leaves, twigs, roots, and habit).
2. Internal or anatomical characteristics which together enable one to perceive anatomical distinctions (anatomical elements of the wood, bark, leaves, and other plant parts).
3. Physiological characteristics which together enable one to perceive physiological differences (growth, development, and reproduction as affected by site factors such as temperature, light, moisture, and soil).
4. Conformity in natural geographical range.

Only through the most careful consideration of all the above can the persistent characters, which alone are acceptable in the recognition of species, varieties, and races, be brought to light. Silviculturally and arboriculturally considered, stability in botanical names is much to be desired. Correct identification of trees and other plants with which foresters work is of fundamental importance. In forest mapping and in the classification of forests into types, a practitioner must know the species. Correct identification is necessary in obtaining seed for direct seeding and nursery work. It is necessary in forest descriptions and

in almost all kinds of research in forests with which foresters are identified.

3. Species

The term *species* has been defined as *the perennial succession of similar individuals perpetuated through reproduction.* This definition is brief and expresses the fundamental concept of a species, namely, continuity of origin and similarity in component individuals. As genetic relationship can seldom be established by observation or historical evidence, it must be inferred from anatomical, morphological, and physiological evidence and from geographical range.

Present evidence brought together by DeVries (1901) and others appears to show that systematic species as accepted by taxonomists are as a rule compound assemblages of plants made up of a variable number of elementary types more or less clearly defined and coming true to seed. Thus among our widely distributed arborescent species the Pacific Coast form of Douglas fir is strikingly different from the Rocky Mountain form. The eastern Texas form of mesquite is strikingly different from the form found in southern New Mexico. Although white spruce and Engelmann spruce are recognized as valid species, yet, where they grow together in British Columbia, systematists have been unable to find persistent characters by which they can be separated from each other. The same is true of jack pine and lodgepole pine.

4. Varieties

A species in which some of its component individuals have characters which constantly vary from the same characters in other individuals is recognized as containing one or more varieties. Varieties occur freely in nature but assume the greatest importance after a species is brought under domestication and is subjected to cultivation. The criterion for a variety is that the deviating characters remain constant through successive generations. In the present concept of a variety it is recognized as similar to the species only with characters plus or minus in the human perception. Most varieties arise from seed variation in the same manner as new species arise, namely, through changes due to differences in habitat, or through mutations.

5. Sport Varieties and Sport Forms

When sport varieties and sport forms are present in tree species, they show deviations from the species in morphological characters but seldom, if ever, in physiological attributes. They produce characters in the

leaves, branches, flowers, or fruit quite unlike those in the parent stock. As a general rule they do not come true to seed but are reproduced in a very small percentage of the descendants, the greater number being similar to the typical form of the species. How these sport varieties arise is not definitely known. Evidence indicates that they are due neither to soil, climate, nor breeding. Where a species may be planted for a thousand generations, the descendants being the mean of the typical form of a species, suddenly there may arise in a plant an abnormal form, a branchless form, a red- or yellow-colored form. There may occur a creeping, dwarfed, bushy, serpentine, juvenile, cleft-leaved, gold-, silver-, or copper-colored, or single-leaved form. For the most part these varieties are very characteristic in that their development is dwarfed as compared with that of the normal form of the species, so that they are useless for forestry purposes. They are, however, very useful for decorative work in landscape gardening. They arise both as bud and seed sports. They are not abundant in nature; in some species, however, they are much more abundant than in others. Mayr (1925) observed 43 varieties of one of the Japanese pines. Although seedlings grown from sport forms give rise to a certain percentage of plants having the characteristics of the sport, they are chiefly propagated through cuttings and by budding on the ordinary form of the species, or on a closely related species.

6. Races

A race of trees within a species or variety is a form which is perpetuated with considerable certainty through the seed. Races are often due to differences in geographical range which cause differences in climate and soil (Schmidt, 1930).

From experiments conducted at Mariabrunn, Austria, Cieslar (1907) has shown the importance of climatic races of forest trees in the practice of silviculture.

From experiments conducted at Eberswalde, Prussia, Dengler (1908) has recorded marked variations in the growth of Scotch pine from seed collected near Eberswalde as compared with seed from more northern localities. Kienitz (1911), in experiments near the same place, records great variation in root and shoot growth, depending upon the soil and climatic conditions under which the mother trees developed.

Huffel (1912), from observations and studies at Nancy, France, shows that the locality from which the seed of Scotch pine is derived affects to a marked degree the quality of the plants grown. Engler (1905, 1913), from a long series of experiments and studies in Switzer-

and, has shown that Scotch pine seedlings decrease in height growth with increase in altitude of the site from which the seed is obtained and with increase in latitude. When grown in Switzerland, one-year seedlings from Scandinavian and eastern Russian seed complete their height growth from one to two months earlier than those from Swiss and German seed from low elevations. On low sites, however, the plants from seed collected on high mountains and in northern latitudes commenced their height growth earlier than plants grown from seed obtained from the lowlands of Middle Europe. The terminal growth of plants from seed collected in northern Switzerland and Germany increased with increased temperature considerably more than plants grown from more northern and from alpine seed. The frequent appearance of top drying on pine in high situations when grown from lowland seed is due to the late cessation of growth.

Trees grown from seed of crooked-stemmed, spreading trees, or of trees otherwise ill-formed because of climate or soil, are for the most part of poor form. When the poor form of the mother tree is due to weather effect or damage by man or beast, the defect does not appear to be carried over into the next generation through the seed.

7. Individuals

The individuals within the species, variety, or race have endless differences. No two individuals of the same species are exactly alike in their outer characteristics and inner development. Are these individual divergences persistent? Are they carried forward into succeeding generations through the seed? Mayr (1925) states that after 10 years of research on these and similar questions at the forest experiment station near Munich the results were all negative. Recent research appears to show that individual variations in trees of the same species, variety, or race, growing naturally under uniform habitat conditions, are not inherited. On the other hand uniform characters which appear in a whole body of individuals of a given species, variety, or race, when grown for generations under one set of conditions, as compared with characters that appear in the whole body of individuals of the same species, variety, or race, when grown for generations under another set of conditions, appear to be inherited. The researches of Zederbauer (1912) indicate that at least in some instances the individual characteristics of the mother tree, such as extreme divergence from typical form of the species, variety, or race, may be transmitted through the seed.

8. Hybrids and Cross-breeds

Usually in nature distinct species do not hybridize; however, there is great diversity in different species in this respect. Many of the various species of willow hybridize freely and reciprocally; others only in one direction. Some species, although very similar in appearance, do not hybridize. In rare cases species of different genera hybridize. The loblolly and longleaf pines and oaks of different species occasionally hybridize in nature. One sometimes finds a hybrid between white oak and chestnut oak, between willow oak and water oak, and between black oak and bear oak, but never a hybrid between a white oak and a black oak. Although on the whole there appear to be but few natural hybrids in forests, the number of closely related species in which the pollen of the one can be made to act upon the ovules of the other by careful technique is very large. Natural hybrids among trees, when they do arise, usually produce seed with a low degree of fertility. The stamens are often impotent. Offspring that arise under the directing power of man and are maintained by skillful and proper handling are considerable in number and of large importance in horticulture but not in forestry.

Crosses are much more prevalent between varieties and races than are hybrids between distinct species of trees. Such unions are termed cross-breeds. They are very common in nature and are a basic force in preventing the splitting up of species into innumerable varieties.

9. TREE FORM

A rigid classification of the diverse forms of woody plants into trees and shrubs is impossible. Many woody plants normally direct a maximum of growth energy into one principal stem from the first and maintain this for many years. Then a tree results, namely, a plant with a well-defined crown upon a woody bole or shaft. Whether it bears all its branches at the top of the bole as in maple or along its course as in spruce and white pine, whether the bole breaks up into forking branches or is traceable to the top of the tree, or whether the tree is short and wide or tall and narrow depends chiefly upon the inherent nature of the tree and is beyond explanation, although partly due to environment. The normal form that a tree assumes may be termed its habit.

Usually the part of a tree above ground is clearly differentiated into a crown and bole; yet in many species grown in the open a definite crown is not developed until late in life, as in many spruces and firs which maintain living branches from base to apex for many years. Even large elms may be clothed with branches quite to the ground. In these

the crown is no longer a head supported at the end of a bole but must be looked upon as distributed over the entire bole.

Deviations from the typical habit of a tree because of natural or artificial conditions often impose upon it the form of a bush or shrub. Thus many species of oaks, birches, and conifers assume the form and proportions of a tree in moist, fertile soil at the lower elevations of their range, but become shrubs on dry, windy sites at higher elevations. The live oaks are often trees 4 feet or more in diameter at breast height in the fertile, moist soil of the low mountain canyons of southern California. On high, dry slopes, both in California and eastward in Arizona, the same species form vast areas of impenetrable scrub 4 to 6 feet high with many stems arising from a common root system. The recurrent breaking weight of snow and ice, the pressure exerted by the wind, the repeated cutting back, due to the browsing of animals or to the interference of man, cause dwarfing and a change in form.

As every species that attains tree size has a well-recognized typical form or habit, a number of type forms are recognized, based on size, shape, mode of branching, and foliage. Among our indigenous trees this type form or habit is a very significant character, as illustrated in the weeping spruce, the fastigiate cedar, the irregular, terraced black gum, the vase-like elm, and the broad, round-headed yellow birch and sugar maple.

Although at first sight it appears there is considerable similarity in habit in most of our trees; yet close study shows consistent differences in the color and lightness of foliage, rigidity and method of branching, size and number of ultimate branches, angle of branch divergence, size and form of the buds, persistency of the leaves, and in a vast multitude of other peculiarities, the summation of which, when accurately perceived and appreciated, enables the distinguishing of one species from another by habit alone. Thus the marked differences in the crown of white oak, sycamore, and sugar maple are largely due to the difference in the angle of divergence of the branches. The chief differences in the crowns of the various species of hickory are in the size of the terminal twigs and the buds. A notable difference in the habit of the crown of larch as compared with that of spruce and fir, aside from the difference in the persistency of leaves, is the dwarf shoots or short branches, so abundant in the former but absent in the latter.

10. Form of Crown

Each species and each variety has a typical form of crown, bole, and root system. One of the most striking characteristics of trees is the great variation in the form of crown of one species as compared with

another. The typical crown form of species and varieties depends upon inner or inherent characteristics. Deviations from the typical are dependent upon external or environmental factors.

The natural tendency of crown form in a tree is seen when it grows in the open. Thus the crown form of sugar maple when so grown is ovoid, that of spruce, fir, and alder conical, that of oak globose, that of hickory columnar, and that of American elm vase-shaped. This natural form is modified by all manner of external influences, particularly by light and wind. Each species and variety has a natural or inherent crown form because the character of the axis within the crown, the method of bud arrangement, the angle of branching, the lateral extension of the branches, and the tendency to produce secondary and tertiary branches do not differ essentially within the species or within well-marked varieties of the species.

The continuous or excurrent axis is characteristic of most coniferous species. It is, however, not uncommon among broadleaved species, as illustrated in red gum, pin oak, yellow poplar, and magnolia. The excurrent axis is characteristic of conical-shaped crowns, particularly up to the time when the principal height growth is attained. Many species with excurrent axes, however, lose their typical conical crown form in old age, because of the elongation of the uppermost branches after height growth is attained. This is well illustrated in white pine, which becomes strikingly flat-topped in old age.

The discontinuous or deliquescent axis is characteristic of most broadleaved species. It is, however, occasionally seen in conifers, particularly in some of the 2- and 3-leaved pines and western junipers. This type of axis is characteristic of a wide variety of crown forms, the different crown forms depending chiefly on the angle of divergence of the branches and their manner of origin.

11. Deviations from Typical Crown Form. — Light is the important influence which causes the crown form of trees in stands to be different from that of the same species or variety when grown in the open. For each, however, there is a crown form for the species or variety in stands which is just as characteristic as that in the open. Competition among trees growing in stands causes the lower branches to die, restricts growing space, and makes the crowns narrower, so long as they are still in the upper canopy. It makes them one-sided and in other ways unsymmetrical. The manner in which competition affects the crowns is typical for each species and variety. When a tree is overtopped the effect on crown form is totally different. Height growth is arrested, the branches spread out laterally, and the crown becomes flat-topped or umbrella-shaped, as in red spruce.

Wind by its mechanical action causes marked deviations from typical crown form. These deviations are most apparent where the wind blows chiefly from one direction and with considerable velocity, as along the sea coast and on the tops of mountains and ridges. They are most marked in trees growing in the open and along the borders of woodland and least marked in trees in the interior of fully stocked forest stands. The deviations from typical crown form arise from the fact that the branches are bent by the prevailing wind from their normal direction of growth and follow the direction of the wind. They become short and thick on the windward side and long and attenuated to the leeward.

When a tree is small, browsing by animals causes the crown to become compact and ball-like and to form close to the ground. This is true for both conifers and broadleaved species, as illustrated in spruce where the terminal bud and the side branches are continually bitten back by deer and also in various species of *Crataegus* when browsed by cattle. The tree maintains its striking ball-like crown until it becomes so large the animals can no longer reach the central shoot, when it begins a rapid height growth with a marked change in crown form.

12. **Effect of Age on Crown Form.** — All species, particularly when growing in stands and when undisturbed by external influences, develop conical-shaped crowns during the early part of life; and as they approach their full height the typical crown form for the species or variety is most apparent and the various types are most easily differentiated. After height growth has been completed the crowns of the trees become wider and rounded off or flat-topped. Some species, however, such as balsam fir and white spruce, retain their juvenile form and even in old age have a narrow, spire-like apex to the crown.

13. Form of Bole

Contrary to crown development, the typical form of bole is exhibited when trees grow in well-stocked stands. The bole is more or less circular in cross section and in form approaches that of a neiloid. The taper is more or less rapid near the ground, is more gradual for the remainder of the clear length, and increases again in the crown. *The ratio between the volume of the bole and that of a cylinder having the same diameter and height is termed the form factor.*

14. **Straightness of Bole.** — Trees tend to grow straight and deviations from straightness are due to both internal and external factors. When deviations arise, because of particular characteristics of climate

and soil, they appear to become fixed by the species, variety, or race growing for generations under similar conditions. Such deviations persist in the offspring when grown in other climates and on other soils.

15. Taper of Bole. — The taper of trees depends upon the rate of growth in different parts of the bole. The bole within the crown exhibits a rapid taper from its base to its top. This is true of all species and is due to the rapid increase in annual growth rings from the top downward through the crown. Taper is less below the crown because of the less rapid increase in growth rings downward. In rapidly growing trees taper is greater than in slowly growing trees because of the differences in the distribution of wood over the growth ring.

16. Cross-sectional Form of Bole. — Form of the bole in cross section is determined both by environmental conditions and inherent characteristics. Most trees are naturally circular in cross section. Many, however, show an inherent tendency toward irregularities, as shown in hornbeam and red cedar and in many tropical species. Irregularities in cross section are more frequent at the base of a tree, as exhibited in buttresses. Damage resulting from death of the cambium on one side of a tree may cause eccentric growth. Twisted grain may cause an eccentric cross section. Trees on side hills have an oval or ovate cross section, due to the greater growth on the lower side. Trees exposed to constant winds have an irregular bole with the greatest growth on the leeward side. Increased growth occurs just below a branch, and hence the cross section is less regular. Economically considered, the form factor of a given species when grown in stands of normal density is far more significant than when grown in the open.

17. Deviations in Bole Form Due to Restrictions in Growing Space. — The characteristics of the bole of a given species can be best observed when a tree is growing in the open. When growing space is limited, the natural tendencies are modified. The tendency in the bole to become modified by restriction in growing space varies greatly with different species. It is greatest in intolerant species and least in tolerant ones. Restrictions in growing space have a tendency to cause the concentration of the crown toward the upper end of the bole, which insures the formation of a long, full-boled stem of the highest financial value. Where the growing space is not restricted the available assimilated nutrients are largely expended in the development of an extensive branch system and a correspondingly short, clear bole with excessive taper.

18. Deviations in Bole Form Due to Age. — All species of trees when grown in the open and in stands of normal density assume a

gradual or more or less uniform taper of the bole until they outgrow the pole stage. It is only later on that they more completely assume the neiloid form. As they approach the limits of age of healthy, vigorous growth the taper becomes less uniform, the portion of the bole below the crown approaches more nearly the form of a cylinder, and the portion within the crown exhibits a greater degree of taper. Within the species or variety, however, the distribution of taper at a given age is largely determined by site.

19. Deviations in Bole Form Due to Site. — Fresh, fertile loam soils as a rule cause a large development of crown and diameter of bole. On sandy soils that are deep and fresh the crown is usually smaller and thinner, the branch development sparser, and the bole of less diameter. The length of bole, however, may be greater and the taper less. On poor, light, sandy soils and on shallow, rocky soils the bole development is usually much inferior in financial value. The bole develops greater irregularities and other defects, its deviation from the circular form of cross section is greater, the clear length is less, and the taper is less regular.

High elevation above sea level indirectly affects bole form in subjecting a tree to greater exposure, more especially to high winds. Not only is the tree dwarfed, and as a consequence the bole shortened, but it is thrown out of the vertical and for this reason becomes very irregular in cross section. There is great irregularity in the width of the growth rings on different radii, as the growth center is far from the geometrical center.

20. Bole Excellencies and Bole Defects. — The study of the origin and cause of poor bole form has been given much attention by foresters, particularly in Europe. Bole form is not only of importance from the standpoint of wood production of the better grades, but it is of equal importance because of its inheritance. Bole form in the mother tree due to climate and soil is a measure of seed quality for that tree. Variations in bole form depend upon both inherent characteristics and environment.

21. Inherent Characteristics. — Among our commercial species three groups may be recognized as of normal bole form, depending on their inherent characteristics. These groups are:

1. Species, which under the most unfavorable conditions of climate and soil and under the most unfavorable method of management, maintain a straight bole. These include all our indigenous species of *Picea*, *Abies*, *Pseudotsuga*, and *Taxodium* and the white pines. If a thousand or more specimens of any of the above are selected at random,

not a single one will have a crooked bole except where the leading shoot has been destroyed. On very precipitous sites, however, the bole may be curved or bent at the base because of mechanical pressure.

2. Species in which the bole is sometimes crooked without apparent external causes. These include: the genus *Larix;* the yellow pines, chiefly those with two or three leaves in a fascicle; and the genera *Tsuga, Cupressus, Thuja, Chamaecyparis,* and *Sequoia.* In all of the above, crookedness may appear in the bole without any apparent external cause. This condition is often seen in larch and in some of the yellow pines, even where grown in pure, even-aged stands.

3. Species in which crookedness is most highly marked. This group includes most broadleaved species. The cause lies in their strong inherent tendency to vary.

From the above it appears that the inherent or inner causes of poor bole form are most pronounced in the third group, less in the second group, and least in the first group. In each group, however, the inherent tendency to deviate from straightness and normal taper is stimulated by over-nourishment, by growing on overly fertile or excessively manured soil; by under-nourishment, by growing on very poor soil; and by growing in a too warm or a too cold climate.

22. **External Influences.** — The external influences which cause crookedness in the bole relate chiefly to climate, soil, and injury to the leading shoot.

Each species has its optimum climate, and it is here that its bole form has the greatest excellence, where it develops the greatest and longest boles, and where the taper is the least and the crown most symmetrical in form. The extreme in poor form, in the crookedness of the bole and in taper and other irregularities, is found at the limits of the distribution of a species. Other things being equal, the greater the humidity of the air is, the better the form and the straighter the bole. Scotch pine is always straight-boled in East Prussia, its region of climatic optimum. White oak has a better bole form in the Ohio Valley in the United States, in Japan, and in southern Europe than elsewhere. The European beech produces a long, straight bole in Denmark, its region of climatic optimum. Scotch pine from Riga in the southern Baltic region has not a single crooked bole in a hundred stems, but this same species planted in central France and southern Germany shows a high percentage of trees having poor bole form, there being from 26 to 37 percent as determined by actual count.

The wind influences the form of the bole and the degree of deviation from the normal for the species. The influence is the greatest on the

side of a forest toward the prevailing wind. The marginal trees are among those of a stand most seriously affected. The percentage of trees on the margin of the stand that deviate from the normal bole form may be three times as many as in the interior of the stand. Thus Mayr (1925) found in his researches near Munich, Germany, that 76 percent of the marginal trees in stands of Scotch pine were crooked-stemmed whereas in the interior of the same stands only 24 percent of the trees were crooked.

The soil can also be the external cause of crooked boles. Trees growing on very stony, shallow soils tend to bend their roots to one side. The boles deviate more or less from an upright position in order to overcome the abnormal position of the roots.

Poor bole form, particularly crookedness, is very commonly caused by damage to the leading shoot or to the terminal bud. This form of damage results from pruning, snow, ice, windbreak, freezing back, fungus injury, and from damage by various forms of animal life, particularly insects. After injury from the above causes, a side branch assumes the position formerly occupied by the terminal shoot and a crook results.

23. Crotched or Double-topped Trees

The crotch or double top usually results from insufficient height growth in early youth; excurrent boles, from the loss of the terminal bud. The double top causes great loss in the quality of the timber. A somewhat similar form of damage occurs in many species when two trees grow close together, either naturally or as a result of clump planting or sowing in seed spots. The loss of the terminal bud very frequently causes double top in pine, spruce, balsam fir, and larch. As a result of inherent tendencies double top is frequent in hemlock, white cedar, maple, ash, and elm. The inherent tendency to form double top is stimulated by an uncongenial climate and an unfavorable soil. The undue development of side branches retards height growth and stimulates the formation of crotches and forking of the bole.

24. Epicormic Branches and Water Sprouts

When the bole is suddenly exposed to light and air by felling the neighboring trees, or when the tree is severely pruned or suffers excessive loss of crown through breakage, insect injury, or damage by parasitic fungi, not infrequently the bole puts out innumerable shoots called epicormic branches, which will more or less impair the quality of the timber. These shoots push their way through crevices in the bark

and often grow more rapidly than the other branches on the same tree.

A careful examination of the place of origin of the buds which give rise to epicormic branches shows that they arise from a crevice behind the crest of a cushion slightly raised above the surface of the bark. This cushion is the mark of a leaf scar so that the bud from which an epicormic branch develops is in reality in the axis of a leaf scar and was formed when the bole or branch was a mere twig in its first year's growth. After the bud had developed, competition for available nutrients forced it to remain dormant. Instead of developing into a shoot it remained a bud but did not die. It elongated just enough each year to keep its apex at the outer surface of the bark of the growing bole or branch. So long as the branch system above the dormant bud maintains its dominance, the bud does not grow out into a branch; but whenever for one cause or another more food materials are available at the particular place than hitherto has been the case, the bud bursts forth and develops into a branch. Not infrequently epicormic branches arise in tufts of a dozen or more stems. This is due to the fact that in some instances the dormant bud, during its years of suppressed growth, forms minute lateral buds at the base of its scales, all of which begin to grow out into branches at the same time.

There is a vast difference in species in their capacity to develop epicormic branches under changed conditions of nutrition. They are extremely common in beech, elm, ash, oak, maple, birch, poplar, and locust. They rarely develop on coniferous species, although sometimes they are found in larch, pitch pine, pond pine, and occasionally in spruce. Water sprouts are very rapidly developing branches. They take the water and nutrients from the crown and may cause a tree to become stag-headed. Epicormic branches often occur in great abundance on intolerant species from which surrounding trees have been removed. They occur in great numbers on the boles of chestnut when damaged by blight.

25. Stool Shoots and Coppice Shoots

True stool shoots arise from the wounded tissue of the cambium, phloem parenchyma, and cortex when exposed. The wounded tissue forms a soft succulent outgrowth known as a callous. The buds which give rise to true stool shoots arise in the tissues of a callous. Although true stool shoots always arise in this manner, a kind of shoot, usually classed as a coppice shoot or sprout, arises from a dormant bud at the very base of the bole, in exactly the same manner as an epicormic

branch. True stool shoots are much less common than coppice shoots. They develop readily, however, from a callous on such species as beech, cherry, alder, birch, and elm.

26. Form of Roots

There is much less known about the form of roots of trees than of the parts above ground. The types of juvenile root form as exemplified in trees have already been discussed. In general, variations in root form as in bole form and crown form depend on inherent characteristics and environment.

27. Inherent Characteristics. — The natural tendency for the roots of all trees is to grow directly downward, develop a taproot, and extend lateral roots equally on all sides because by so doing a tree gains firmer support and generally obtains more soil moisture and nutrients. There is, however, a great difference in typical root form in different species and varieties, which is particularly recognizable in the early life of a tree.

There is a distinct correlation between roots and crown. If the roots are reduced in size or capacity, the crown is reduced by the death of a portion of the branches. If the crown is reduced below the capacity of the roots, there is a tendency to an increase in the crown by the development of epicormic branches and water sprouts. If the crown is increased by stimulated growth after a stand is thinned, the roots increase proportionately and reestablish an equilibrium between crown and roots.

28. External Influences. — The external influences which cause deviations from the normal root form for the species or variety relate chiefly to the soil. The roots of some species have greater power of accommodation to soil of different depth and character than have the roots of other species. Some trees, such as black walnut, require deep soil; others, as illustrated by red maple, send down deep roots when the soil has sufficient depth but can also grow in swamps, where the effective soil is very shallow. The depth of root penetration in peat and swampy soils is determined mainly by the height of water table, and the root systems of trees growing in these soils are far more spreading than those of the same species growing in heavy-textured soils (Korstian, 1924; Korstian and Brush, 1931; Rigg and Harrar, 1931). When a tree grows in a soil best suited to it, the form of root is typical for the species. When the soil is less favorable the roots tend to a greater development in the most favorable horizon where the required moisture and nutrients can be obtained and at the same time the trees

be supported. If there are rocks or other obstructions in the soil, the roots must grow around them in order to absorb the necessary nourishment and moisture. Roots in sandy soil spread out much more than in a more compact soil. The root system of a tree growing in a stand of normal density has a tendency toward greater restriction in lateral expanse through competition with the roots of surrounding trees. The tendency is for the roots to spread into soil as yet unoccupied, because of the greater amount of available moisture and the larger amount of soil nutrients.

29. GROWTH AND DEVELOPMENT

The most obvious characteristics of a tree are growth and the unfolding of new organs. Growth in trees is very conspicuous, owing to its rapidity and long duration. The term growth as usually employed implies both increase in size and the formation of new organs. As sometimes used, however, it is confined to increase in size and is synonymous with increment or accretion. The formation of new organs is distinguished as development.

The tree as an individual has its beginning as a single cell. In order to attain its ultimate size and maturity it must grow. It must become larger and undergo differentiation. It becomes larger by the multiplication and expansion of cells. There is an increase from the original cell through cell division, the daughter cells ultimately attaining the dimensions of the mother cell. Increase in size continues as long as there is cell division and cell expansion.

From the earliest stage of a tree throughout its entire life it is a product of growth and development, a product of increase in volume and differentiation. During the earlier period of its life it is an embryo within a developing ovule which later matures into a seed. During this period it is attached to the mother tree and draws its subsistence therefrom. As soon as the ovule matures and becomes the seed, it usually falls from the tree, and the contained embryo lies dormant for a more or less extended period of time with the life processes mostly at rest. The ripening of the seed, therefore, marks the period which separates the time when the young tree receives its nourishment from the parent and the time when it receives nourishment from outside sources. Germination begins the independent growth of the individual tree which through its entire course of later existence is shaped not only by inherent forces but by the factors of the site as well. A tree is early composed of two essential parts, namely, the shoot, or part above ground, and the root, or part below ground. The shoot grows upward and develops a

more or less expanded system of branches and foliage, through which a tree is supplied with carbon dioxide from the air. The roots grow downward, afford stability, and develop a more or less expanded system of branches and root hairs, through which a tree is supplied with nutrients and water from the soil. It is from these materials and carbon dioxide that a tree synthesizes its food.

As a tree develops, the various physiological functions require a division of labor. This results in a differentiation of structure and the formation of tissues. Consequently a mature tree exhibits a great variety of tissues of different structure, performing different kinds of work. Thus the bark, cork, cuticle, and epidermis are protective tissues; the sclerenchyma and collenchyma are strengthening tissues; the parenchyma and, to some extent, other cell forms are metabolic tissues; and the stomata and lenticels are aerating organs.

As a tree grows older it spreads out laterally both above and below ground. The shoot continuing upward in its growth throws out side branches and increases in foliar expansion. As this process goes on, the lower branches are supplied with successively smaller amounts of nutrients and ultimately die and fall away. In this way the bole and crown of a tree are formed.

Early in the life of a tree the taproot extends downward, varying greatly in growth in this respect in different species, and a system of lateral roots and rootlets is developed which affords the tree a greater absorptive surface in the soil horizons that contain the greatest amount of water and nutrients.

As long as a tree continues to develop, living tissues must be protected, metabolic processes must go on, and nutrient-containing water must be conducted to all parts. The nutrients contained in the soil water are taken up by the roots, enter the transpiration current, and are carried to the leaves where they are enriched by the carbon products of photosynthesis. By chemical transformations they become the elaborated food for all the living tissues.

Anything which interferes with the movement of the nutrient-containing water from the tree roots to the foliage, or which checks the movement of the elaborated food supply, kills or injures a tree. Thus when a tree is girdled, if the cut is made through the sapwood, the tree dies because no water reaches the crown above. If the cut is made only through the bark, the tree does not die immediately but is finally starved; the roots are deprived of the elaborated food, which is conducted down the bole through the inner bark.

30. Periods of Rest

The growth and development of a tree does not proceed uniformly. It is profoundly influenced and controlled by external conditions, many of which show a decided periodicity; consequently growth and development exhibit a corresponding periodicity (Howard, 1910). The first conspicuous period of dormancy is from the time of maturity of the seed until growth is reestablished by germination. Many forest trees retain their fruit for long periods after maturity. Black locust and catalpa do not cast their seed until late winter or early spring following their maturity. A number of conifers, including jack pine, lodgepole pine, Monterey pine, and sand pine, often retain their fruit for 10 or more years after ripening. The seeds of these species remain dormant, or nearly so, for long periods without losing their viability.

There appears to be a great difference in the seeds of the various species of trees in their power to retain their viability over extended periods of time. To a very large degree viability depends upon the temperature and moisture conditions to which the seed is subjected. The seeds of some species, however, lie at rest in the litter or soil under conditions moderately favorable for germination, for a period of one or more years after they mature and are disseminated. They appear to require a more or less extended period of after-ripening before germination will take place. When dense regeneration appears after denudation of an area occasionally some of it may result from seed that has been lying dormant in the soil for one or more years. The removal of the vegetation and the exposing of the soil to light and to higher temperature awaken the seeds from their dormant condition, and germination occurs. Southern white cedar may spring up in dense stands following clear cutting in this forest type and subsequent exposure of the site to increased heat, moisture generally being adequate or in excess (Korstian, 1924; Korstian and Brush, 1931). At least some of this reproduction originates from seed remaining one or more years in the litter and peat of the forest floor. On the other hand, Douglas fir seed not destroyed by birds, insects, and rodents either germinates or decays within a year after it falls, both under virgin timber and on open cut-over areas (Isaac, 1935, 1943). Western white pine seed showed 25 percent viable after two winters' storage and less than 1 percent after three and four years' storage and only an occasional viable seed thereafter, while the seed of western hemlock, grand fir, and western larch did not retain viability longer than the normal one-winter period (Haig, Davis, and Weidman, 1941).

In a given lot of seed within the same species the period of dormancy, even under conditions most favorable for germination, varies considerably. Some seeds will germinate as soon as they are subjected to favorable conditions of heat, moisture, and air; others will lie dormant for months when subjected to identical conditions. If a viable seed immediately after ripening fails to grow when planted under conditions favorable to germination, it may be said to require a period of rest; it may have an immature embryo or an impervious seed coat, or its failure to germinate may be due to a combination of an impervious seed coat and a required rest period. The rest period appears to be a physiological condition which inhibits germination immediately after maturity. Although the resting period may be due to internal causes, failure to germinate may also be due to external causes, namely, unfavorable heat, moisture, and air conditions (Crocker, 1916; Korstian, 1927; Spaeth, 1934; Toumey and Korstian, 1942).

Although popularly speaking the seed represents a dormant stage in the development of a tree, life processes do not entirely cease even when the seed is in storage. Respiration and transpiration still go on, increasing or decreasing with the increase and decrease in temperature and humidity. Tashiro (1912) has observed by the use of special apparatus that even dry seeds give off definite amounts of carbon dioxide as long as they are alive.

Periods of rest that follow germination are more or less seasonal. This seasonal dormancy or cessation of growth is common to all species and on all sites. It is most marked, however, in trees growing in regions having well-defined cold and hot seasons. Even in cold regions, however, the vital processes do not wholly cease. The roots may continue to grow during a part or the whole of the cold season, and there is more or less loss of water through transpiration throughout the year. In the study of almost 300 species of woody plants Howard (1910) found that nearly all have a rest period, of varying length in different species. Thus in some species it is only a few days, while in others it is several months. Certain species like willow were forced into growth at the early part of their rest period; others, such as hickory and walnut, Howard was unable to start by his methods before the end of the normal rest period. On the other hand, Kramer (1934), working with yellow poplar, red oak, white oak, beech, and red gum seedlings, found that, while exposure to low temperature and treatment with ethylene chlorhydrin were both effective in breaking dormancy in advance of the usual time, the most rapid response and most vigorous growth were obtained by exposure to low temperature followed by treatment with

ethylene chlorhydrin. Klebs (1914) induced the buds of resistant European beech to open at the most unusual times by powerful electrical illumination.

From extended studies on the periodicity of root growth in silver fir, Scotch pine, and several other European species, Engler (1903) found that the production and development of roots are not continuous. Root growth is interrupted by periods of repose which do not exactly correspond with those when the shoots are at rest. Engler found that in Switzerland the growth of the roots of coniferous species is suspended from November to March or April, whereas root growth in the deciduous trees does not appear to cease entirely even in mid-winter. However, the period from early February to the beginning of March is the least favorable for root growth, owing to low temprature of the soil. In general, root growth begins its rapid development a few days to several weeks before the buds start. It was found that the roots cease growth in summer because of drought, but in October there is a new period of activity, which is much more intense and more prolonged in deciduous species than in conifers. Studies by Stevens (1931) in New Hampshire show rapid growth of white pine roots in the spring and autumn and a distinct tendency of the growth rate to slow down during midsummer. Root elongation in this species does not entirely cease until the soil freezes. Reed (1939) found that root growth of shortleaf and loblolly pines in central North Carolina did not cease entirely, even in the coldest parts of the winter.

31. Growth Rings

Seasonal periods of rest result in the woody tissue of all exogenous species being laid down in more or less clearly differentiated growth rings. When one ring is formed each year it is known as an annual ring. This is the case in exogenous trees in most parts of the United States because here we have well-defined hot and cold seasons. When, for one cause or another there is more than one growth period in a single year, the growth rings do not correspond with the annual rings. When two or more growth periods occur within a year, the rings are less clearly defined and the additional ones are known as false rings. In regions where the seasons do not exhibit well-marked changes in temperature, as in the tropics, the growth rings are always more or less poorly defined or, rarely, absent.

The innermost layers of the growth ring are laid down at the beginning of the growing season and are composed of more or less open, thin-

walled cells of springwood. The summerwood cells laid down later are usually much thicker-walled. The distinctness of the growth ring, therefore, depends upon the difference in density between the springwood and the summerwood. The difference has been attributed to the pressure exerted by the bark, which is less at the beginning of the growing season. The growth rings are of considerable importance to a forester. They not only enable him to determine the age of a tree with considerable accuracy and the favorable or unfavorable conditions of each year for the production of wood, but they are also an index of the quality of timber.

32. Longevity and Death

The cycle of development, in spite of all that can be done, sooner or later comes to an end and the tree perishes. There appears to be no inherent reason why a tree should die. The tissues are continually undergoing change and are continually being repaired; they are for the greater part renewed annually. Although living and dead tissues form in a tree a sort of unity which often endures for centuries, in the course of time the living cells become reduced in number and finally die; the tree decays and disappears. As the tree becomes old and large it is increasingly more difficult to supply the extremities with needed materials as the roots and leaves become separated by wider and wider intervals (Coulter, Barnes, and Cowles; 1930–1931). As the live branches are higher and higher above the ground and become more widespreading, mechanical overthrow threatens more and more, and other physical conditions which a tree must resist in order to survive become more severe.

Although the meristematic tissue in a tree is commonly believed to retain its embryonic condition unchanged and there is nothing in the living parts that determines the end, foresters and nurserymen hold that vegetatively propagated trees tend to run out and that coppice reproduction becomes poorer and poorer with successive crops, as if through senility. Benedict (1912) holds that from his experiments it appears that vegetative propagation can not produce a young plant, in the sense of juvenility derived from seed germination.

Although there appears to be no inherent reason why a tree should die except the possible senility of meristematic tissue, the causes of death due to injury and disease are many. As a tree becomes old, the rate of growth decreases and its power of recuperation from damage becomes less and less. Species which best resist damage and have the greatest power of recovery from injuries live the longest. So also indi-

viduals of a given species, which escape or are protected from injuries, live longer than those exposed.

The more important factors which influence the duration of life in trees are:

1. *Species.* There is a great difference in the average age that different species of trees live and in the maximum age that they are capable of attaining. Duration of life is, therefore, a well-recognized characteristic of each particular species.

2. *Durability of wood.* Species with durable wood as a rule live much longer than species with wood that decays very readily.

3. *Strength of wood.* All trees are more or less exposed to the force of wind and possible damage by snow and ice. Trees with strong, elastic wood resist such forces better than those with brittle wood. Thus, for example, hickory and oak are much less damaged than poplar or birch.

4. *Power of recuperation.* Some species have the inherent power to recuperate after damage much more rapidly than others. Rapidly growing trees recover better than those of slower growth.

5. *Power of resistance.* Different trees have different powers of resistance. Insufficient growing space results in diminished development and, if prolonged, may affect longevity. The power of resistance is believed by many to be weaker in nursery-grown trees than in those resulting from natural seeding.

6. *Site conditions.* Longevity within a species depends very largely upon favorableness of climate and soil. A tree of a given species, growing under optimum site conditions, lives longer than one of the same species less favorably situated.

7. *Damage.* A tree so situated that it escapes damage which causes breakage of limbs or abrasion of bark, through which infection may occur, lives longer than other individuals less fortunately located.

8. *Origin.* Trees originating from seed are much longer-lived than those derived from stool or root shoots and from suckers and cuttings. For this reason trees of a high forest are much older at maturity than the same species grown as coppice.

The absolute duration of life of a tree is of minor importance in forestry as compared with the length of time that it remains vigorous and sound. It is, therefore, not only necessary to consider the absolute duration of life but also the age at which the various species, under different conditions, begin to become unsound and otherwise deteriorate. One should also consider the age of a tree at the time of maximum seed production and reproduction and greatest vigor from stool shoots

because one of a forester's first obligations in making fellings is to cut the crop at a period of its life that will result in its being replaced by one as good or even better.

33. Classification of Species and Varieties on Basis of Duration of Growth. — Duration of growth is measured by longevity. The 20 species enumerated below, when classified in order of duration of growth, are:

1. Coniferous species: white pine, hemlock, red pine, white cedar, red spruce, red cedar, pitch pine, and balsam fir.
2. Broadleaved species: white oak, sugar maple, beech, yellow poplar, red oak, sweet birch, shagbark hickory, chestnut, American elm, cottonwood, butternut, and gray birch.

34. Determining Age of a Tree. — The exact age of a standing tree can not be determined by direct observation after the crown has become well elevated above the ground. In young trees the number of branch orders and sometimes the number of successive whorls of branches along the axis are a fairly accurate record of age. In many species, as in white pine, the whorls of branches or traces of them are recognizable, particularly where a tree is growing in the open, up to the time that it is 50 to 60 years old. In estimating the age of trees by the number of branch whorls, 2 to 4 years should be added to the number of whorls in order to allow for the growth of the seedling when no branches were formed or when those formed were too small for the scars to be discernible in later years. However, in some species, such as loblolly pine, shortleaf pine, and chestnut oak, two or more whorls of branches are developed in one growing season, which makes this method of determining age very unreliable for these species.

The age of standing trees, having distinct growth rings, can be accurately determined by means of careful borings made from the circumference of the bole to the growth center. These borings are made with an increment borer which removes a small core of wood reaching from the bark to the heart. The number of annual rings in this core plus a variable number representing the age of the tree at the time its height was the same as the height of the boring above the ground is a measure of age. An increment borer is impractical for use on trees much more than 18 inches in diameter. Where there is no record showing when a tree first started its growth and the annual rings are indistinguishable, there is no known means for determining the exact age of large trees. The size of a tree of a given species under a particular condition of growth, the form of crown, the shape of bole, and the texture and color of bark may indicate the approximate age.

35. Rapidity of Growth. — Growth varies in rapidity, depending on both inherent characteristics and environment. The most important factors which account for variations in the rapidity and duration of growth are:

1. *Species and variety.* Each species and variety has its own characteristic rate of growth. In general, long-lived species and varieties make a smaller total growth in a given period than do short-lived trees. Thus aspen, although a smaller tree at maturity, makes a much larger total growth in 50 years than white oak, which is a much larger tree at maturity. Intolerant species usually grow much faster than tolerant species, although the growth is not as well sustained. Thus yellow poplar, a moderately intolerant species, grows much more rapidly than sugar maple, a tolerant species.

The maximum size that a tree attains is determined by both its energy and duration of growth. Thus many short-lived species, such as aspen, butternut, gray birch, and pin cherry, although exhibiting great growth energy, never attain large size; on the other hand, long-lived species like white oak and sugar maple are slow to reach massive proportions.

2. *The soil.* There is for each species and variety a certain quality or condition of the soil under which it makes the best growth. Deviations from the optimum for the species or variety cause a falling off in the intensity of growth. Although most species make their best growth on a deep, fertile, moist, loam soil, there is great variation in different species in this respect. Thus a soil which sustains an inferior growth in ash and walnut may produce optimum growth in white pine.

3. *Climate.* For each species and variety there is a certain optimum climate under which it grows best. In general the rapidity of growth of a species in the juvenile stage, other things being equal, depends on warmth of the site. At an intermediate age and later it depends upon climate corresponding in temperature to the optimum for the species or variety. A temperature higher than the optimum increases growth but shortens its duration. A temperature colder than the optimum retards growth.

4. *Degree of competition for root space and crown space.*

5. *Age of tree.* The rapidity of growth in all species is influenced by the age of a tree. Growth is at first slow but after the first few years rapidly increases with age up to the maximum, which is usually attained late in the life of a tree, after which it falls off with more or less rapidity.

6. *Individual variation.* Each individual within the species or variety exhibits inherent tendencies which cause it to vary more or less

from all other individuals. It can not be said that the most slowly growing trees always grow slowly because of differences in climate, soil, and other characteristics of the site.

7. *Interference with normal development.* Anything which materially interferes with the normal development of a tree, such as transplanting, pruning, and defoliation, retards growth.

36. Classification of Species and Varieties on Basis of Growth Energy. — The classification of species on the basis of growth energy is impracticable for regions exhibiting great variations in climate and soil. Thus the rate of growth of ponderosa pine in the Black Hills of South Dakota is different from the rate of growth of the same species in California. The rate of growth of the canyon live oak in the low mountains of California is different from the rate of growth of the same species on the high mountain slopes. Although it is impracticable to classify species in accordance with their growth energy for whole countries, such a classification is highly useful for species within a climatic type or included in a single forest type. Thus on the upland glacial soils of southern Connecticut 20 species between the ages of 15 to 30 years, on the basis of their relative growth, may be arranged in the order of their greatest growth, as follows:

1. Coniferous species: white pine, red pine, pitch pine, hemlock, balsam fir, red spruce, white cedar, and red cedar.
2. Broadleaved species: cottonwood, gray birch, butternut, American elm, chestnut, sweet birch, red oak, sugar maple, hickory, beech, and white oak.

37. Growth Characteristics of Chief Importance

Growth characteristics of chief importance to a forester relate to the bole of a tree, more particularly to height, diameter, taper change, and the resulting increase in volume. These vary in diverse ways depending both on internal characteristics of the species, variety, or race, and on external influences. The form of the bole at different ages is determined by height growth and by diameter growth at different points along its axis. Internal characteristics which control growth relate to characteristics derived from inheritance. Thus one species, variety, or race, growing under the same conditions of soil and climate as another, has an inherent tendency for greater height growth. Another has an inherent tendency for greater diameter growth. One species, variety, or race may inherit a tendency to develop a bole more nearly approaching a cylinder in form. Our various species, varieties, and races exhibit great differences in height and diameter growth and in form of bole due to inheritance.

External influences which control growth are indefinite in number and relate to conditions imposed on the tree after germination takes place. Thus crowding trees in the stand stimulates height growth at the expense of diameter growth. Crowding from one side induces eccentric growth. Overtopping reduces diameter growth at the base of the bole and shortens the axis within the crown.

38. **Height Growth.** — The growth of a tree in height depends on the energy and duration expressed in development of the leading shoot. It depends on the progressive unfolding each year of a terminal bud or a strong lateral bud which develops into a leader. Each year, a bud is formed at or near the end of the leader which continues its upward growth the following season. Before the bud begins to unfold in the spring, formative tissue is already there. As the bud unfolds and new growth begins, there is both the formation of new cells and the enlargement of those already laid down. These soon become separated into different tissues to perform special functions.

Rapid growth in length of the terminal shoot usually takes place during the first few weeks after the bursting of the bud. This enlargement is chiefly due to the expansion of cells already there. In some species early spring growth may exceed an inch in length in 24 hours.

Two forces are at work as the buds swell: one an upward thrust of the growing apex of the shoot as it elongates, and the other an outward thrust of the expanding leaves and stem which forces the bud scales apart. As each bud unfolds, the scales at its base are pushed outward, but generally they do not appreciably enlarge; neither is there as a rule any appreciable elongation of the internodes between them. The changes in the bud scales and in the length of the internodes above the basal scales are usually very marked. The scales usually become progressively larger and the internodes longer until the normal leaf and the normal length of internode for the species are attained. The extension of the shoot begins in early spring, reaches a maximum in a few weeks, and may cease altogether or be very slow after mid-summer.

The intensity and the duration of shoot elongation during the growing season are very largely determined by the character of the growing shoot, namely, whether it is of determinate or indeterminate growth.

39. Determinate Growth in the Leading Shoot. — In species like pine, spruce, oak, and yellow poplar, all the structures of the developed terminal shoot are packed away in the bud in embryonic form. These rapidly expand and reach their full size in a variable length of time after the bursting of the bud. Further elongation of the shoot is impossible until a new terminal bud with its rudimentary struc-

tures is formed. Growth in length is arrested, therefore, for the time; buds develop and the tissues mature.

The period of repose usually continues until the following spring; not infrequently, however, two or three periods of growth, alternating with periods of repose, take place in a single growing season. Thus, very frequently one finds two or even three periods of rapid growth alternating with periods of repose in red oak seedlings, the first year from seed. Each period of elongation of the shoot is followed by the development of a terminal bud and the ripening of the tissues; sometimes, however, the last growth is killed by early autumn frosts before the tissues have had time to ripen. When such is the case the axis is continued the following season by the development of a lateral bud. The stimulation of a leading shoot of determinate growth to make a second or even a third growth in a single season is largely due to the moisture conditions and warmth of late summer or early autumn.

When the growth and development of the terminal bud of the leading shoot is from the outset more vigorous than that of lateral shoots, a slender, conical crown usually results, as illustrated in white spruce and pin oak. When the growth from the terminal bud has little or no preeminence over that of some of the other buds, as white oak, the crown is usually broad and round-topped without a well-defined axis.

40. Indeterminate Growth in the Leading Shoot. — In many species without true terminal buds, as illustrated in ailanthus, black locust, and osage orange, there are no alternating periods of rapid elongation of the leading shoot and periods of repose. The growth is more or less continuous throughout the growing season; new growth continues to unfold at the apex of the shoot until late summer. As the end of the shoot does not come to rest and harden its tissues before the beginning of the autumn frost, it is generally killed and as a consequence the axis the following spring is continued by the unfolding of a strong lateral bud just back of the dead tissue. The axis is crooked and the crown irregular and unsymmetrical.

In most species of indeterminate growth, like elm and basswood, the end of the shoot just above a strong lateral bud withers and drops away in the autumn, and the axis is continued the following spring by the development of this bud. Because of the withering and dropping away of the end of the shoot, this lateral bud has the general appearance of a true terminal bud. Its nature can be readily recognized, however, by the scar left by the casting of the end of the shoot.

41. Annual Height Growth. — The actual length attained in the annual growth of the leading shoot varies from a mere fraction of an

inch to several feet, depending partly on inherent factors and partly on external conditions. As a rule, after the first few years, height growth rapidly increases a little each year until the maximum annual height growth is attained. Although the time varies in different species and on different sites, maximum annual height growth is attained early, usually when a tree is in the pole stage. After the maximum is attained it is continued with but little variation for some years, after which it decreases with more or less rapidity.

The rapidity of height growth from the seedling through the pole stage appears to be closely correlated with the capacity of a species to endure crowding from the side. The excessive early height growth of the intolerant gray birch, cottonwood, and pin cherry enables them to rise rapidly out of the undergrowth and reach the light above their competitors. The slow, early height growth of the tolerant balsam fir, hemlock, and beech does not cause their death even when they are below their competitors and completely dominated.

42. MAXIMUM HEIGHT. — The maximum heights attained by different species and the heights attained in different periods of time and under different conditions are of vast importance from the practical silvicultural standpoint. The total height attained by a tree is measured by both the rapidity and duration of height growth. Although the gray birch grows very rapidly in the juvenile stage and outstrips most of its competitors, the duration of life is so short that it seldom attains a greater height than 40 to 50 feet and is ultimately driven from the stand by the competition of more slowly growing species having greater duration of growth, such as white pine. Even though the juvenile height growth of gray birch is greater than that of Douglas fir, the latter species maintains vigorous height growth six to ten times as long and, consequently, although growing more slowly at first, may reach a maximum height of 385 feet (Harlow and Harrar, 1941).

Although each species has its inherent rate and duration of height growth, in which the intensity, during the early stages of life, coincides with the demands made by a particular species for space, some species like sugar pine, larch, and yellow poplar, continue their early attained dominance throughout life, whereas others are ultimately overtopped, because of lack of persistency in height growth.

A tree does not continue to increase in height throughout its entire life. The height may actually decrease in old age, owing to dying back of the top. Later it may continue its increase by additional height growth from a lateral bud. Thus in old age the total height continually varies, first in one direction, then in the other. This is due to the weak-

ened vitality of a tree when a series of adverse years may cause the dying back of the top; but a later period of good years may cause a continuation of height growth.

43. Diameter Growth. — In all species of forest trees, growth in girth is approximately proportional to growth in height, as they are both the expression of the vigor of an individual tree. As long as a tree lives there is usually added each year a new layer of wood entirely about it and a new layer of bark. These new layers are the product of cambial activity and are laid down between the old bark and the old wood. As cambial activity is largely measured by the available food supply, the width of the growth ring in a species is dependent upon the relative size and exposure of the crown and upon the extent of the root system (Fritz and Averill, 1924). It also varies with climate and soil. Under uniform climatic and soil conditions trees having the greatest growing space increase much more rapidly in diameter than the same species in a crowded forest. Trees on warm sites make more rapid diameter growth than the same species on cold sites. Diameter growth is also influenced by soil moisture and soil nutrients. A warm season increases diameter growth, provided there is adequate moisture. Often, however, a hot year is accompanied by little diameter growth because it is also a dry year. Adequate summer moisture is a most important factor in sustaining diameter growth throughout the growing season (Douglass, 1928). Interseasonal variations in diameter growth are most marked on dry soils, and least on wet soils. So also seasonal variations are the greatest on dry soils. Checking of diameter growth during a heavy seed year is due to the consumption of the reserve and newly elaborated food materials in the production of seed. Defoliation by insects may not kill a tree but it checks diameter growth. Various tree diseases, by interfering with the normal life processes, reduce diameter growth. Forest fires reduce diameter growth by injuring the tree and by causing deterioration of the soil. Destruction of organic matter by fire exposes the soil to drying and hardening and it is likely to become overrun with exhausting forest weeds; as a result, diameter growth is reduced. The lengthening of the season is favorable only when it begins early. When a tree grows in a crowded stand, diameter growth is more seriously checked than height growth; but when the growing space is more than sufficient for the normal development of a given tree, growth in diameter is stimulated at the expense of growth in height.

44. Effect of Age on Diameter Growth. — The natural tendency in a tree grown from seed in the open is to make a small annual diameter

growth at first, which gradually increases up to the maximum for the site. The maximum is commonly maintained with little variation for many years, usually until long after the principal height growth has been attained, after which it drops off with more or less rapidity. The youthful period of slow diameter growth is usually longer than the period of slow height growth, and the period of maximum diameter growth is always later than the period of maximum height growth.

In comparing the rate of growth at different periods in the age of a tree, it should be borne in mind that the width of annual ring does not represent in itself the actual productive work of a tree. The wood formed each year is a continuous layer over the bole, branches, and roots. It is evident, therefore, that as a tree becomes larger, the same quantity of material makes a thinner layer over the surface. If the progress of growth in diameter and volume is compared, it may be seen that volume growth continues to increase for many years after annual diameter growth has begun to decline.

45. VARIATIONS IN DIAMETER GROWTH IN DIFFERENT PARTS OF A TREE. — The width of the growth ring at the stump is different from that half way up the bole, and the latter is different from that in the crown and root (MacDougal and Shreve, 1924). The bole may be considered as composed of three parts, namely, the portion within the crown, the portion from the base of the crown to the swelling of the butt, and finally the swollen butt. The relative thickness of the growth ring in each of these parts varies with the dominance of a tree. It is different in dominant trees from that in subdominant trees, and different in subdominant trees from that in overtopped trees.

In dominant trees the relative thickness of the growth ring in the three parts of the bole conforms to the following characteristics. Within the crown the growth ring is thickest near the base and decreases progressively toward the top of the crown. In the part between the base of the crown and the swelling of the butt the thickness of the growth ring generally increases downward; but in dense stands it may tend to decrease downward. The thickness of the growth ring at the butt is greater than in any other part of the bole. In subdominant trees the relative thickness of different parts of the growth ring conforms to the following characteristics. Within the crown it is the same as in dominant trees; in the clear bole the thickness of the growth ring is practically uniform from the crown to the butt; and there is an increase in the thickness of the growth ring in the butt. In overtopped trees the diameter growth of the axis within the crown is the same as in dominant and subdominant trees; the diameter growth of the clear bole decreases

from the base of the crown downward to the butt, and in some instances there is no diameter growth at all at the butt.

The variations in the thickness of the growth ring in one part of a tree as compared with another, when grown under different conditions, have been a matter of discussion and observation for many years. Although various explanations have been offered, it would seem that the distribution of diameter growth in a given tree is determined by its specific needs. The growth energy exhibited at a given point is determined by a stimulus at that point. In every tree there is a difference in the stimulus at different points, and the distribution of nutrients and the intensity of growth at a given point depend on the character and intensity of the stimulus. The greatest diameter growth does not occur where the nutrients happen to occur but where, owing to stimulated energy, they are drawn.

The chief stimulus in localizing diameter growth appears to be external strain. The tree in its process of development is subjected to a great variety of strains, largely due to wind action. It must produce a form which will resist these strains, otherwise it will be unable to endure. The strains due to wind are different in intensity in different parts of a tree. The strain is greatest at the base. This results in the greatest thickness of the growth rings at this point. The above mechanical theory explains in a satisfactory manner the variations in the distribution of growth over the annual layer. It also explains the eccentric growth of the bole. Thus a tree on a steep hillside usually exhibits a greater radial growth on the down-hill side; the pith is nearer the bark on the up-hill side. This is due to the leaning of the tree and the greater strain on the lower side. The compression of the tissue is a stimulus for increased diameter growth on that side. Trees may also have more foliage and therefore produce more food on the down-hill side. In the same way a tree exposed to prevailingly high winds has most foliage and thickest growth rings on the leeward side; desiccating winds cause reduction in foliage on the windward side. A tree at the edge of a stand may exhibit the thickest growth rings on the side toward the open, owing to the heavy branches on that side and the constant strain in the bole due to them. For the same reason the thickest growth rings are found on the lower side of a branch. Wide growth rings are localized on the bole just beneath the origin of the branches.

Variation in the density of the wood in different parts of the bole is probably also due to differences in mechanical strains. The wood in the butt is denser and tougher than elsewhere in a tree and this is particularly true of trees growing in open stands. There is considerable

difference in the density of the wood on different sides of a tree when the bole is unsymmetrical.

46. Taper Change. — As the cubical content of the bole depends on taper as well as height of a tree and its diameter at the stump, this factor must be considered in determining volume. Each species has a characteristic form of taper which varies with age of stand, density of stocking, and quality of site.

The typical form of taper of a given species is shown in a tree growing in the open, in its region of optimum growth and on the best quality sites. This typical form of taper is an internal or inherent characteristic and is modified in various directions by external or environmental conditions. Furthermore, it varies with age of tree. In general, taper is the greatest, at a given age, in a free standing tree and becomes progressively less with the increase in density of stocking. In dense stands, the clear bole approaches more and more the form of a cylinder. Taper in trees of a species at a given age rapidly increases with adverse climatic and physiographic conditions of site.

Taper of the bole in all trees in youth approaches that of a cone, in which there is a uniform and gradual decrease in diameter from the base to the apex. As a tree becomes older, however, and particularly when grown in stands, and the crown is progressively raised higher and higher above the ground, the form of bole departs more and more from that of a cone and becomes more or less neiloid in shape near the base. There is a rapid taper at the butt due to root swell. The clear bole above the root swell approaches more and more the form of a cylinder or the frustum of a paraboloid. Taper in that part of the axis which extends through the crown increases toward that of a cone.

47. Volume Increase. — The increase of a tree in cubical contents, or its volume increment, is the final expression for growth in height and cross-sectional area at various points along the axis. The object of most studies in height and diameter growth is for the determination of volume and the prediction of future yields in volume. In trees growing in the open and in stands that have been adequately opened by thinnings, the maximum volume increment takes place but a few years before the economic maturity of a tree. Various external factors which cause irregular fluctuations in height growth and diameter growth likewise cause changes in volume growth.

48. Quality Growth. — Quality growth relates to growth into useful and more valuable sizes. It is a function of time and the distribution of mass in a tree. Quality in an individual tree means increase in value per unit of volume, because of size, freedom from defects, and regularity

and distribution of growth. The most important factor in determining the quality of an individual of a given species in a stocked stand is size. The proportion of bark and sapwood to heartwood rapidly decreases with size.

Age affects quality not only on account of its relation to size but also in its relation to defects. A young tree is seldom free from defects, particularly knots which tend to weaken it and interfere with the ease with which the wood can be worked into forms for use. An old tree is subject to defects, owing to damage from fungi, insects, and other external agents. Quality, therefore, is a function of age in that it is low during the period of principal height growth, rapidly increases during the period of principal diameter growth, and rapidly declines during the period of decline in the vigor of a tree. Uniformity in annual growth, particularly in diameter, affects quality, more especially in species which exhibit considerable variation in the density of the wood with variation in the width of the growth rings. The more uniform the growth, the higher the quality of the wood. Silvicultural treatment aims to crowd trees close together during their period of rapid diameter growth in order to reduce the width of the growth rings; and, later on, when under natural conditions diameter growth slows down, the treatment aims to stimulate diameter increase by progressively opening up the stand by thinnings. The distribution of growth over the tree determines the relative proportion of limb to body wood and the form, length, and taper of the clear bole.

49. Reproduction

Reproduction is a vital process exercised by every self-perpetuating species and variety. Were it not exercised they would soon pass out of existence, because the life of every tree is of limited duration. Through reproduction, the species, variety, and race are continued from generation to generation. The formation of an independently existing offspring necessitates its separation from the parent tree. This is usually brought about in the seed, which is most often a product of sexual reproduction. Sometimes, however, it is brought about vegetatively. For instance, the formation of a bud is not distinguished as reproduction so long as it remains attached to the tree as a part of the whole. Should the bud in one manner or another become detached and develop as an independent tree, this is then termed vegetative reproduction. The most common form of vegetative reproduction of forest trees that occurs naturally is by root suckers and stump sprouts. Sometimes

twigs and even large branches become detached and later take root and grow into independent trees, as in cottonwood, willow, and elm. In other cases pieces of detached roots develop buds and grow into independent trees. Occasionally embryos are developed in the seed without the intervention of pollination. This often occurs in the hackberry. Here they arise vegetatively, usually from buds which originate on the inner wall of the tissue surrounding the embryo cavity.

In vegetative reproduction the growth and development of the parent plant is directly continued, and the new plant partakes of all the individual characteristics of the single parent. In sexual reproduction, on the other hand, the new plant exhibits characteristics of both parents, although not a mean between them. Reproduction from the embryo developed in the seed through pollination shows greater variations between individuals than reproduction from sprouts or other vegetative parts.

50. Seed Production. — The formation of seed depends largely upon the amount of reserve carbohydrates and nitrogenous materials stored in a tree. These vary greatly, depending on inherent characteristics and external factors. In general their relative abundance depends on:

1. The species or variety.
2. Age of tree.
3. Condition of soil.
4. Climate, particularly the temperature of the growing season.
5. Extent of crown and root space.

Part of the reserve food material stored by a tree during any given season is used the following season for the production of new growth. It is not, however, all put to immediate use for this purpose. Some remains in reserve and is used for growth when conditions are unfavorable for the elaboration of new material. In the early period of a tree's existence and through the period of principal height growth the reserves of elaborated food are chiefly used by a tree for increase in its vegetative parts. After a time, however, which varies with different species, the accumulated reserve is largely used in seed production. After a tree produces a heavy crop of seed, it usually requires a period of several years for the accumulation of sufficient reserve food to make another heavy seed crop possible. This explains the reason why heavy seed crops seldom occur 2 years in succession. Trees begin to bear seed when a sufficient amount of reserve material has accumulated. Sprouts have been known to bear seed in the second year. Young lodgepole pine has been found in the open, bearing seed at 6 years, red

spruce at 15 years, pitch pine at 10 years, and southern white cedar at 4 to 5 years.

Staminate cones in abundance have been observed on 3-year-old jack pine seedlings growing in seed beds near New Haven, Connecticut. Mature cones of white pine have been collected in plantations 5 years after planting. The stock was 3 years old (2–1) when planted.

In general, the most abundant and best seed is produced after the principal height growth has been attained. It is then that the crown begins to thicken and the energy of a tree is at its best. Trees continue, however, to bear seed until very old. Large-crowned, dominant, or open-growing trees maintain their seed-bearing power just as they maintain large growth in volume.

Recent evidence indicates that strong, vigorously growing, young Norway pine trees (sometimes conveniently called "vegetative") produce generally weaker seed and seedlings than trees of the same or greater age, whose vigor has been reduced by any one of several causes (Bates, 1931). Vigorous seed trees produce weak seedlings, and weak seed trees produce strong progeny, at least in the sense of early survival and without particular regard to hereditary tendencies which may develop later. Whether inhibition of vegetative vigor and hardiness in seed trees is a result of old age, competition of other trees, deficient moisture, poor soil, or other causes, the seed produced by slowly growing trees is, for the most part, of an entirely different quality, better filled and nourished than that from very vigorous young trees. However, the better seed frequently shows a definite dormancy after maturation and apparently requires an after-ripening period prior to germination. Bates (1931) believes that, while seed trees and their environment are in such condition as to permit and encourage rapid growth in the parents, either the food materials produced by the trees themselves or the nutrients derived from the soil are not available in sufficient quantities to produce good seed of high vitality, or are diverted more readily into the channels supplying the vegetative tissues, which really means essentially the same thing.

The chemical and physical character of the soil has a direct bearing on the quantity of seed produced, as it helps to determine the amount of reserve food materials stored in a tree. The amount of ash constituents in seed is large, and for this reason a soil deficient in potash or other essential mineral elements in available form produces poor crops of seed. Seed also contains large quantities of nitrogen; hence soils deficient in this element in available form, owing to repeated forest fires, grazing, or removal of litter, produce trees which yield small,

inferior crops of seed. Other things being equal, the more fertile the soil, the heavier the seed production, because of the larger and more rapid accumulation of reserve food materials.

The carbon-nitrogen ratio profoundly affects seed production. High carbohydrate production, partly influenced by the rate of photosynthesis, depends on crown space and weather conditions. It is favorable to seed production. Soil rich in available nitrogen is favorable to vegetative growth and unfavorable to seed production.

In general the yield of seed is greatest from trees growing within the climatic optimum for the species. All species are poor seed bearers at the northern extremities of their ranges, owing largely to the season's being too short for the full maturity of the seed. At the southern extremity of their ranges they often bear full seed crops, but the seed is likely to be infertile. Furthermore, the vigor of the tree is soon exhausted. Under excessive humidity many seeds are sterile, owing to imperfect pollination. Excessive aridity reduces the quantity of reserve food, thus greatly reducing the yield of seed.

One of the foremost factors in determining seed production is crown and soil space. Trees growing in the open produce seed earlier, in greater abundance, and oftener than trees growing in stands. Crown space causes large crown development and increased assimilation. Reserve food materials are quickly stored in excess of those required for growth and normal vegetative development. Zon's (1915) studies on the seed production of western white pine show that the yield from carefully selected trees on sample plots varies with the different crown classes. Thus, in natural stands of the above species, 98.8 percent of the yield was obtained from the two upper crown classes. The remaining three crown classes produced a yield of but 1.2 percent of the whole, although they included more than one-half the total number of trees.

When trees grow in stands, seed production is confined to the tops of trees. When they grow in the open it is distributed over the entire crown. Overtopped trees bear few seeds. Tolerant species may exist for 100 years or longer under the crowns of other species without bearing a single crop of seed, as often in red spruce and hemlock in New England.

CHAPTER XIV

DIFFERENTIATION AND DEVELOPMENT OF STANDS

Since a forest consists of a land area covered with trees dense enough to form stands, the stand, along with the individual trees forming it, becomes one of the most important units of treatment in silvicultural management. *A stand is generally defined as an aggregation of trees occupying a specific area and sufficiently uniform in composition (species), age arrangement, and condition to be distinguishable from the forest on adjoining areas* (Soc. Amer. Foresters, 1944). Sometimes, however, stands are segregated on more or less artificial bases and are then only of local importance. For example, purely for organization purposes, an intensively managed forest organized for continuous production may be divided by roads, trails, streams, or artificial boundaries into compartments and stands, rectangular or more or less irregular in shape and variable in size. A forester finds that an intimate acquaintance with the stands comprising a forest is not only essential in the treatment and management of the forest but is also very useful for purposes of more specific description.

1. DIFFERENTIATION OF STANDS

Stands are differentiated on a number of bases, among which the following are the more important:

1. Age.
2. Composition.
3. Density.

2. Differentiation of Stands on Basis of Age of Component Elements

When a stand varies little in age of trees composing it, it is termed even-aged. How much variation in age there may be between the trees of a stand which is still classed as even-aged varies somewhat with the method of management and rotation. As a general rule a difference of more than 15 years in the age of individuals in an artificial or second-growth stand will throw it out of the class of even-aged stands; on the other hand a difference of 25 years, or more, in the age of individuals in

virgin stands need not throw them out of the even-aged class or the regular form of high forest, when considered from the standpoint of forest management.

When a stand varies in the age of individuals, it may include trees of all age classes or part of the age classes may be omitted. In an all-aged or selection form of forest stand the different ages are mixed together either individually or in groups. A stand in which some of the age classes are lacking is irregular; it is not even-aged nor yet of all ages. Two or more age classes are well represented but not all.

3. DEVELOPMENTAL STAGES IN STANDS

Not infrequently reproduction following a severe forest fire forms a complete stand in a comparatively short time. Thus a stand of paper birch on an old burn is usually composed of individuals of approximately the same age. Likewise white pine and other species may completely occupy idle agricultural land and lumbered areas within a period of 10 to 15 years after cultivation ceases or lumbering takes place. These stands are even-aged.

In an all-aged stand there are no recognizable stages of development from seedlings to mature trees, so far as the entire stand is concerned. Many ages are present most of the time. In even-aged stands, on the other hand, well-differentiated stages of development are recognized because only one age is present at a time. The stages of development in even-aged stands are:

Seedling Stage. This stage extends from the time of germination up to the time when the stand begins to close. It usually covers a period of from 5 to 15 years.

Thicket or Sapling Stage. This stage begins with the closing of the seedling stage and ends with the elevation of the crowns well above the ground and usually with the death of many lower branches.

Pole Stage. This stage begins with the closing of the thicket stage and ends when the height growth begins to decline. During this stage the boles tend to clear of branches and attain most of their economic length.

Young Timber Stage. This stage begins with the falling off in height growth and ends when height growth is fully attained.

Mature Timber Stage. This stage begins with the completion of height growth and ends with the beginning of deterioration in the product. This is the period of principal diameter growth and quality increment.

Over-mature Timber Stage. This stage begins with the start of deterioration in the product or with the first stage of decline in the stand. It is a period of little or no growth and progressive decline in quality increment.

From the standpoint of size, in commercial species, an individual tree is often considered a seedling when developed from seed and less than 3 feet tall; a small sapling when 3 to 10 feet tall; a large sapling when over 10 feet tall and less than 4 inches in diameter breast high; a small pole when 4 to 8 inches d.b.h.; a large pole when 8 to 12 inches d.b.h.; a standard when 12 to 24 inches d.b.h.; and a veteran when over 24 inches d.b.h.

4. CHARACTER AND FORM OF AN EVEN-AGED STAND

The character and form of an even-aged stand depend very largely on whether the stand is composed of a single species or a mixture of species. Competition is keener when only a single species is present. It is the least intense for a given density when there are a number of species each of which makes different demands on the site.

In an even-aged stand of a single species the individuals become more and more variable in size as competition forces dominance in some and suppression in others. The size of each particular individual composing an even-aged stand depends upon:

1. Its inherent capacity for growth.
2. The degree of competition.
3. The favorableness of its particular location.

Some individuals have descended from more vigorous stock, from trees of better form and more rapid growth. It is but natural that such individuals should attain dominance over less favored individuals, even where they are growing under equal conditions as to competition and degree of favorableness of location. The individuals, other things being equal, that encounter the keenest crown and root competition fall behind their competitors in growth. The individuals that chance to reach the superior location from the standpoint of light, moisture, and nutrients soon outgrow their associates. From the above it may be seen that even under most favorable conditions a stand begins to differentiate from the standpoint of dominance as soon as it closes and there is competition among the individuals for crown space or for root space. Even before the stand closes there is more or less differentiation because of inherent differences in individuals for growth and local variations in site factors.

A relatively even-aged stand may show as great a variation in the size of individuals composing it as an uneven-aged stand. Thus relatively even-aged mixed stands of spruce, balsam fir, and paper birch that become established on burns in the Laurentian region of Quebec, when 75 years old have an overstory of birch with the dominant trees 10 to 15 inches in diameter and 60 to 75 feet tall and an understory of spruce and balsam fir in which the trees are 1 to 4 inches in diameter and 6 to 20 feet tall. In the Adirondack Mountains red spruce, under the deep shade of a virgin overstory, has not attained a height of 3 feet in 50 years, whereas trees of the same species growing on similar sites in the open attain heights of 40 to 60 feet in the same length of time.

5. Advantages of Even-aged Condition of Stand

Many arguments have been advanced by practicing foresters for and against even-aged stands. Such stands are either of a single species or a mixture of species. Of a single species are the stands of second growth white pine in New England and loblolly pine in Maryland, Virginia, North Carolina, and many other parts of the South. Even-aged natural stands of hardwoods from seed and sprouts are usually mixed, as illustrated in many of the hardwood stands in southern Connecticut. The advantages from even-aged stands depend somewhat on the species and the quality of site. With suitable species grown under acceptable site conditions, an even-aged stand usually results in the following advantages:

1. A larger number of crop trees per acre and greater uniformity in size.
2. Better development of the bole because each tree is surrounded by trees of the same age, grows to greater height, and has a longer clear length. The bole is straighter and has less taper.
3. Better natural pruning, owing to more intense competition in the crop trees.
4. A reduction in size and less variation in the crowns. The branches are also smaller.
5. A better quality of product and a better form of bole, owing to a more uniform rate of growth.
6. A greater uniformity in thinnings. Thinnings are more easily made and usually are more profitable.

The above desirable features can not be attained under all conditions. The preservation of an even-aged mixture in desirable proportions through all stages of development becomes increasingly difficult as the species vary in tolerance, height growth, and crown form. The preservation of a pure even-aged stand through all stages of development and in a satisfactory condition of growth and vigor depends upon its ability

to maintain quality of the site. Even-aged mixtures of tolerant species, such as sugar maple and beech, sugar maple and red spruce, beech and hemlock, sugar maple and white pine, are usually acceptable. Even-aged mixtures of tolerant and intolerant species permit great variety when suitable selections are made. Uneven-aged stands sometimes produce timber of better quality than even-aged stands. Thus young white pine that starts in small openings in uneven-aged mixtures of hardwood and pine has straight boles and small, thin side branches. Natural pruning is excellent, and the taper is relatively small. The high quality of mature white pines intermixed with hardwoods of varying ages is due, in part at least, to their starting in small openings.

6. Disadvantages of Even-aged Condition of Stand

Although a number of advantages may result from an even-aged condition of the stand, particularly economic ones, there are also certain disadvantages. In other words, uneven-aged stands usually have certain desirable qualities which can not be attained so well in even-aged stands. The more important of these are:

1. The soil is better and more uniformly protected in the uneven-aged stand because the trees fall in several crown classes, and as a consequence the canopy is deeper. Furthermore, the protection is uniform from year to year, whereas in even-aged stands it varies from year to year, depending upon the stage of development of the stand.
2. With the removal of mature trees in the uneven-aged stand, natural regeneration of tolerant species is easily attained, because of the large number of trees left on the ground; in the even-aged stand there is often little or no advance reproduction for a second crop. In many instances, however, abundant advance reproduction appears in even-aged stands of white pine, red spruce, ponderosa pine, and in a number of other species after the principal height growth has been attained.
3. The uneven-aged stand offers greater resistance to injury from wind, snow and other external agents.

7. DIFFERENTIATION OF STANDS ON BASIS OF COMPOSITION

The trees forming a stand may consist of a single species of silvicultural or economic importance or two or more species may be present. The former stand is *pure;* the latter stand is *mixed.* When each unit is pure but of different species from those of adjacent units, the forest is mixed by stands, groups, strips, or clumps, instead of by individual trees. The terms pure stand, pure group, and pure strip, do not mean

in the practice of forestry that only one species is present but rather that only one species of economic or silvicultural importance is predominant.

In estimating timber for commercial purposes a stand is usually classed as pure when 80 percent or more of the overstory is of a single species and forms practically all of the commercial product. On the other hand 10 percent, or in some instances less, of a highly valuable species in the overstory throws the stand from the pure to the mixed class when considered commercially. When 5 percent, or even less, of the total number of trees per unit of area is composed of a second species it may suffice to throw the stand from the pure to the mixed class, if this small percentage is silviculturally important. Thus a forest of white pine and beech with 5 to 10 percent of beech forms a mixed stand because the beech is a permanent part of the stand and has a marked silvicultural effect on the pine. On the other hand, a forest of white pine and gray birch with 20 percent of gray birch is usually considered a pure white pine stand, owing to the temporary presence of gray birch in the stand.

Silviculturally considered, the mixture may be in the crowns or one species may form the overstory while the second forms an understory. An overstory of oak with a well-developed understory of beech is a mixed stand; an overstory of oak with a natural, fragmentary understory of birch, hop-hornbeam, and shrubs which have no economic value and little silvicultural importance is usually considered a pure stand.

Mayr (1925) states that in order to have a real mixed alliance, the mixture must be in the crowns, and there must be real competition. When the crowns of one species are entirely under the crowns of another, he states, there is not a real mixture but a pure stand, pure group, pure strip, or pure clump, with an understory of another species. The authors disagree with the above interpretation of a pure stand because an understory of a second species is often of great silvicultural importance and often determines the character and quality of the overstory.

From the above it appears that there is no arbitrary rule which determines the percentage of subordinate species that must be present in order to constitute a mixed stand. Sometimes the predominant species need form but 80 percent of the stand in order that it be classed as pure; in other stands more than 95 percent of the trees present must be of a single species.

8. Pure and Mixed Natural Stands

Pure stands are the exception rather than the rule in virgin forests. There are, however, many notable exceptions, as illustrated by the vast areas of ponderosa pine in New Mexico, Arizona, and eastern Oregon, also by longleaf pine in the Gulf States and by red spruce on many mountain slopes in New England. Pure stands usually occur where the site is only suitable for a single species or where one species through competition brings about the absence of all others. Their most common occurrence is in young even-aged stands that have become quickly established after denudation. Thus the stands of jack pine, lodgepole pine, loblolly pine, red spruce, and aspen that follow denudation are nearly always pure. Intolerant, thin-foliaged species like gray birch, aspen, and black locust seldom form pure stands in natural forests except when young and following denudation. On the other hand, tolerant, densely foliaged species, such as hemlock and beech, may maintain themselves indefinitely in pure stands. Pure forests are most frequently found in nature, growing in alpine regions and in other localities where the weather is cold. Even the most tolerant species seldom grow in pure stands in tropical and subtropical regions. The climax forest, however, is seldom pure although ponderosa pine in pure stands is the climax in New Mexico, Arizona, and Oregon, and red spruce in places in New England. The most common forms of the highest type of mesophytism in the deciduous hardwood forests of the eastern United States are not represented by single species like maple, chestnut, oak, hickory, and ash but rather by a mixture of two or more.

Although the mixed stand is the most frequent form of natural forest there is much controversy on the part of foresters regarding the advantages and disadvantages of pure stands both from the standpoint of timber production and of economic superiority (Nisbet, 1893).

9. Occurrence

Occurrence relates to the manner in which trees are assembled in the stand. The distribution of trees in a stand is described by the terms frequency and abundance. Frequency refers to the number of places where individuals of a given species are found within the unit, and abundance refers to their relative abundance or the actual number of individuals present. Thus in our eastern hardwood forests sassafras and red mulberry are frequent species, but they are never abundant. On the other hand, black oak and sugar maple are often abundant.

From the point of view of occurrence the trees in a stand or other forest unit belong to the following classes:

1. *Gregarious.* When a species occurs naturally in pure stands. The term is applicable to such species as white pine, lodgepole pine, red spruce, hemlock, and aspen. It is not necessarily applicable to pure stands artificially established.
2. *Consorting.* When a species grows in mixtures but forms a considerable part of the crop as is usually the case with beech, sugar maple, white oak, hickory, and chestnut.
3. *Concomitant.* When a species grows in mixtures but forms only a small part of the crop as is usually the case with black walnut, black cherry, basswood, and red mulberry.

10. Mixtures by Individuals and by Groups

The very fact of the frequently mixed character of a climax forest argues the beneficial effect of each species in the mixture on the others or the presence of each making it possible for the others to persist. In stemwise or individual crown mixing, each individual of each species is brought into contact in the crown with individuals of other species. Thus each is influenced in the highest degree by other species in the mixture. When crown mixing is by pure units the contact of tree crowns within the unit is with crowns of the same species. The crowns of different species are only in contact on the periphery of the units. The inner portions of the units have the characteristics of pure stands. Necessarily, the larger the units, the more closely the entire forest partakes of the characteristics of pure stands. The smaller the units, the nearer it approaches the mixing of species by individuals.

Although in the mixing of groups and similar units the interior of the unit has characteristics of a pure stand, under the influence of the species in adjacent units it partakes somewhat of characteristics of individual mixing, particularly so far as relates to storm resistance and insect damage. When the stand or group is more than one or two acres in area, the influence of the trees on the circumference on those in the interior, and the influence of those in the interior on those on the circumference, is negligible, unless the pure units are very long and narrow.

11. Fundamental Principles Underlying Natural and Artificial Composition of Stands

The development of pure and mixed natural stands, the number of species in mixed stands and the development of artificial stands in pure and mixed form are largely determined by the following considerations:

1. Mixed forests are predominant in warm regions; so also the warmer the region the greater the preponderance of individual mixing, as in the sub-tropical forests of southern Florida. The colder the climate the greater the frequency of pure stands and the less the frequency of mixing by individual stems, as illustrated in pure forests of pine and spruce in Canada. Sometimes soil conditions may counteract the warmer climate to produce pure stands, as in the mangrove and longleaf pine forests in the Gulf States.

2. The natural tendency of all tree species in their region of optimum development is toward pure stands as they have advantages over other species not in their region of optimum development. Deviations from the optimum in either direction cause the stand to lose more and more its tendency to develop in pure form and the individuals of the species to become isolated between the individuals of other species better adapted to the site. Thus white pine often grows in pure stands in the Lake States and elsewhere in its region of optimum growth, but it occurs as isolated individuals at the outskirts of its natural range.

3. Usually the better the physical characteristics of the soil and the higher its fertility the more certainly will either a pure or mixed stand when removed come back to the same species as before denudation, provided the stand is climax for the site. The complete removal of a stand of spruce, fir, and hemlock from any of the deep, fertile soils in western Washington is almost immediately followed by a young stand of the same species. In moist tropical regions, however, a new crop of the same species seldom follows clear cutting. Usually a jungle of inferior species appears first.

4. The poorer the soil quality, as illustrated in overly dry soils, loose soils, and sandy soils, the less the mixture of tree species and the greater the tendency toward pure stands, as illustrated in pure jack pine stands on the sand plains of Michigan and pure stands of longleaf pine on dry, sterile, sandy soils in Georgia.

5. Soils which have been mismanaged through clear cutting and the removal of the litter, or by frequent burning, have a tendency toward pure stands because the soil can sustain a relatively small number of species. This is illustrated in the pure stands of aspen that follow repeated fires in Colorado and the pure stands of paper birch that follow repeated fires in northern New England.

6. All species of trees can grow in pure stands but only a relatively few can, in the process of development, prevent other species from entering and changing them to mixed stands. Therefore, many species are grown in pure stands in artificial forests that are not in pure stands

in natural forests. Thus catalpa, black locust, and walnut are often planted pure, yet they do not occur in pure stands in nature.

7. Tolerant species tend to develop in pure stands to a greater extent than do intolerant species. Root and crown competition, in stands of a single tolerant species, inhibits intolerant species from entering, but tolerant species can readily enter stands of intolerant species.

8. Certain chemical characteristics of the soil, as illustrated in an overabundance of salt, overwetness of the soil as in swamps, and an acid condition of the soil characteristic of moor and heath, tend toward the formation of pure stands by excluding all but a few species with special adaptations to overcome the adverse conditions. Black spruce and American larch, characteristic of peat soils, often occur in pure stands in the Adirondack Mountains and in New England.

9. As a general rule, mixed stands are composed of species belonging to more or less widely separated genera. When composed of species of the same genus the mixture is more likely to be by groups or clumps. Thus in southern New England red oak is on the lower slopes where the soil is deep, white oak on the middle slopes, and post oak and chestnut oak on the dry ridges. These four species are seldom found mixed by individual stems.

10. The wider the anatomical and morphological distinctions and the nearer the growth characteristics of two species the better do they grow in mixture, as illustrated in the tolerant species, beech and red spruce, and in the less tolerant white pine and red oak.

11. Pure stands are usually attained in silvicultural operations by artificial regeneration or by special silvicultural methods, tending toward rapid natural reproduction. Slower methods of natural reproduction are more likely to give mixed stands which are silviculturally better than pure stands when the mixture is well arranged.

12. Differences in Reaction of Pure and Mixed Stands

Stands of a single intolerant species are most densely closed during their early stages of development, namely, through the young pole stage. Later crown density becomes broken, branch arrangement irregular, and the boles usually remain short. Grass and other herbaceous plants appear on the forest floor.

Even-aged stands of a single species of intermediate tolerance remain closed throughout the pole stage, the boles become more completely cleared of branches, the soil remains for a longer time free from herbage,

and the litter remains normal, although in some stands raw humus appears. From this time forward, however, the grass and other herbage is the same as in the stand of a single intolerant species.

Stands of a single tolerant species remain closed throughout all stages of development. They attain full branch development, full bole development, and full height. Coniferous species, however, tend to develop an undecomposed acid litter (raw humus) which retards growth and may be unfavorable for natural reproduction. Broad-leaved deciduous species maintain a loose, open soil usually without the formation of raw humus.

Stands of a single species, either tolerant or intolerant, suffer more from external agents such as storms, snow, ice, water, avalanches, land slides, insects, and fungi, and they are favorable to the increase of animal and plant parasites. Furthermore pure stands offer but little opportunity to foresters for treatment. The management is extremely simple, compared with that of mixed stands.

13. Formative Ability of Different Species When in Stands

Each species has within itself the power to develop a more or less definite form of bole and crown. Deviation from the normal type in one direction or another is chiefly due to variations in climate and soil, and to damage from external agents. Furthermore, the form and growth characteristics that a species assumes because of peculiarities of climate or soil, through natural selection, may be carried over in the seed and reappear in the succeeding generation.[1] Thus in tolerant conifers the power to produce good quality is diminished on poor soil, and this tendency may continue over into the next generation. Mayr's (1925) studies on the shallow, gravelly soils near Munich, Germany, show that among the dominant stems of Scotch pine, 60 percent are of poor form and 40 percent of good form, the high percentage of stems of poor form being due to poor soil. With the same species on better soil 60 percent of the dominant stems are of good form. Mayr points out that when the two intolerant species, Scotch pine and European larch, are grown in mixture, particularly in warm climates, their formative ability is exceedingly poor, a remarkably small number of stems attaining good form. In warm climates the formative ability of the larch is somewhat better than of the pine, the former having about

[1] The influence of site, especially climate and soil conditions, upon the progeny of forest trees has been discussed by Toumey and Korstian (1942) and Baldwin (1942).

70 percent of good to 30 percent of poorly formed boles. The formative ability of white pine and Douglas fir is excellent, as a very high percentage of the boles grow straight under widely different conditions of climate and soil. Far more attention than at present should be given to the formative ability of important species in silvicultural practice.

14. Directing Composition of Stands

Silviculturists should be able to encourage or discourage the degree of purity in stands by cleanings and thinnings, thus favoring one species or another to the disadvantage of other species in the mixture. Thus an even-aged mixed stand of many species, when taken in the seedling thicket, and pole stages, can be transformed into a pure stand in a relatively short time by the gradual removal of all but the desired species. A mixed, uneven-aged stand is much more difficult to transform and requires a much longer period. An unfavorable pure stand can not be developed into an acceptable mixed stand. Favorableness and unfavorableness in mixed stands are expressed most in mixture by individuals, less in mixture by groups or strips, and least in mixture by stands, and for the following reasons:

1. The unfavorable silvicultural effect, predominant in pure intolerant stands, relates primarily to the form of the bole and to soil deterioration. Unfavorableness decreases when species of intermediate tolerance are mixed with intolerant species and is entirely eliminated when intolerant species are managed in mixture with tolerant species.
2. The unsatisfactory development of pure intolerant stands after the early pole stage can be corrected through the introduction of tolerant species to form an understory and to afford soil protection.
3. The unfavorable development of pure tolerant stands can be corrected through individual crown mixing with other tolerant species, but better with intermediate and best with intolerant species. In this way the volume increment lost to the single tolerant species by the addition of the other species can be balanced or increased by the growth of the introduced species. Thus the volume lost in a stand of tolerant beech can be more than made up by the increase in volume of introduced yellow poplar or ash.
4. Intolerant species are unsuitable to crown mixing. An intolerant species forming the upper story and a tolerant species forming the lower story is ideal for obtaining the largest yield from the intolerant species.
5. When two or more species that make widely different demands on soil moisture or soil nutrients are grown in mixture, the mixture

should be by groups rather than by individuals, each species occupying the soil best suited to it. The greater the variation in soil requirements in these particulars, the greater the necessity for mixing by groups.

6. The relative proportion of intolerant trees in the stand should be governed by quality of soil. The better the soil, the greater the number. The disadvantages of a stand mixed in the crowns, insofar as they relate to quality of product, decrease with decrease of intolerant trees in the stand.

7. The crown mixing of partly tolerant species is usually advantageous on good soils, as it tends to increase the relative proportion of stem wood to branch wood, over that of most other mixtures.

8. The crown mixing of tolerant species like spruce, balsam fir, beech, and maple, is usually good practice and beneficial results commonly follow on all classes of soils. Pure stands of tolerant species, however, produce as high a product in volume and quality as mixed stands of tolerant species, provided quality of the site is equally well maintained.

9. The reproduction of acceptable mixed stands is much more difficult, much slower, and calls for greater skill by foresters than in the reproduction of pure stands. Furthermore, pure stands, although often silviculturally inferior, are sometimes preferred for economic reasons.

10. In general, the fitness of a species to be raised in pure stands depends upon its capacity to improve or at least maintain quality of the soil. The exceptions are: (*a*) where imperfect canopy and the resulting scarcity of humus do not materially injure the stand, as on very deep fertile soils that have ample moisture; (*b*) when the stand is managed under a short rotation and harvested before excessive openings occur in the canopy; (*c*) when the particular site will produce but one species of economic value, as sometimes on overly wet sites; (*d*) when but one species is merchantable and silvicultural fitness is sacrificed for economic superiority.

11. Mistakes made in the selection of species can be more easily corrected in mixed stands because those least suitable can be removed in thinnings.

15. Pure Stands as Compared with Mixed

In the regeneration of forests a decision must be made between the development of a pure or a mixed crop for each particular site. In making this decision, Mayr (1925) emphasizes the importance of a knowledge of:

1. The climatic and soil factors of the site in order to judge whether all the species will grow equally well.

2. The habit and growth characteristics of the species in order to know whether they can be brought to economic maturity best in pure stands or in mixed stands.

Species differ greatly in their requirements for growth and development. They differ greatly in height, diameter, and volume growth. Some grow slowly; others grow with great rapidity. They exhibit great variation in tolerance and longevity. Because of these and other differences some species can be brought to economic maturity in pure stands; others form successful stands only when mixed with other species. On the whole, mixed stands present a more complete utilization of the site and are more productive.

In general, good silviculture and forest protection demand mixed crops; forest finance often demands pure crops. One can obtain the advantages of both pure and mixed forests by groups of pure stands, each surrounded by other species in accordance with the demands of the site. The almost insuperable difficulties, however, in managing a large forest cut up into small pure groups usually make the application of this method impracticable.

16. Dependent Species in Pure Stands

Although most tolerant species may be grown as pure crops, dependent species[1] should be grown in pure stands only under the following conditions (Heyer and Hess, 1906, 1909):

1. Under short rotation for special purposes, namely, when the intention is to harvest the crop before the canopy has opened up excessively. This is illustrated in growing catalpa and black locust for fence posts under a rotation of 12 to 25 years.

2. Where the rotation is for a long period with the expectation of underplanting the dependent species when the canopy becomes too open properly to conserve the quality of the site. This is illustrated in growing larch, white oak, black cherry, walnut, and a great variety of other species, which, 20 to 35 years after planting, open up too much to sustain an adequate layer of forest litter and humus.

3. On sites where the soil is sufficiently deep and fertile to maintain good growth, even with imperfect cover and deficiency of humus. This

[1] A dependent species commonly relies upon the assistance of its associated species and therefore grows best in mixture with one or more of the principal species which are capable of forming pure stands without assistance from other species (Nisbet, 1894).

is illustrated in successful pure stands of walnut on the deep, fertile bottomlands of eastern Nebraska and Kansas where the ground water is but 8 or 10 feet below the surface.

4. Where the particular site is suitable for a dependent species only, or where it can find a ready market, or can be used for a special purpose.

17. Advantages of Pure Stands

Although, silviculturally considered, pure crops are usually undesirable, there are often economic advantages which overbalance silvicultural disadvantages. The most important of these advantages are:

1. Management is much simplified and thinning operations require less skill.
2. Natural pruning is generally more uniform than pruning in mixed crops. However, when an intolerant species is mixed in the crown canopy with a tolerant species, the pruning of the intolerant species is superior.
3. The crop can be harvested more economically and only the species grown which command the best market.
4. Artificial restocking is simpler, usually less expensive, and the resulting stand is usually more complete.

Because of the above advantages, particularly the much less experience required to bring pure crops to maturity, regeneration in pure stands is usually encouraged in the United States. Imperfect knowledge of the silvical characteristics of our native trees mitigates against regeneration in mixtures. Wrong species for mixtures are often selected and early cleanings and thinnings can not be made. Under present conditions, therefore, it is sometimes safer to regenerate all but the dependent species in pure stands. Even with dependent species, only in exceptional instances should more than two species be planted in mixture. Furthermore, it is usually much safer to seed or plant dependent species like larch, oak, walnut, cherry, yellow poplar, and ash in pure stands with the expectation of underplanting with a tolerant species when the soil begins to deteriorate than it is to run the danger of using wrong species in the mixture.

Although silviculturally considered, the mixed stand is ideal, the practice both in the United States and abroad often has been to replace the original mixed stands with single species. This has been particularly true of white pine, Norway pine, ponderosa pine, Engelmann spruce, and Douglas fir in the United States and Scotch pine and Norway spruce in Europe. The ease with which pure stands can be

artificially established, their uniform and rapid juvenile growth, and their early promise of yielding large financial returns on the investment are important reasons for their formation.

The formation of pure stands, however, is sometimes indicative of insufficient silvicultural knowledge on the part of foresters. As we gain more definite knowledge of the silvicultural requirements of our economic species, mixtures will be established with greater confidence and with greater assurance in the final results.

In France, where silviculture is well understood and practiced, mixed stands form about three-fourths of the forest. Even in Germany, following the leadership of Gayer (1898) there has been a strong reaction against the establishment of pure forests. Even such tolerant conifers as spruce and fir are grown more and more with from 10 to 15 percent of hardwoods. Gayer (1886) states that the leading principle in the rational and economic treatment of forests must be less in the direction of pure than of mixed crops, and that the degree to which and manner in which mixed stands occur throughout any system of management must be considered as the best test and standard by which the results of management may be judged.

18. Advantages of Mixed Stands when Correctly Made and Maintained

When the advantages of pure stands as noted above are compared with those from acceptable mixed crops as given below, it appears that the latter are not only superior silviculturally, but when mixtures are correctly made and maintained are likely to be of superior economic value as well. The more important advantages that may result from mixed crops are:

1. Where a mixture is suitably arranged the site is most completely utilized. The most complete utilization of a given site for forest crops demands that each varying portion be stocked with the species best suited for growing thereon. When mixed by groups or clumps on particular soils best suited for each, the forest as a whole maintains a better canopy and for a longer time than do pure stands. When so treated, the forest not only utilizes the productive capacity of the soil to a higher degree but is also better able to conserve it. The fact that the various species in an acceptable mixed stand draw upon different soil horizons and have different requirements for light and nutrients argues for a greater density of crop under the same degree of competition. The more dense canopy of the mixed stand becomes of constantly increasing

importance as the crop increases in age, and it is chiefly the prolonged maintenance of canopy which gives many mixtures their superiority.

2. A mixture of shallow-rooted species with deep-rooted species forms a stand that suffers less from wind and more fully utilizes the soil. Pure stands of shallow-rooted species like balsam fir and red spruce suffer severely from windthrow. When these and other species of like root habit are cut, leaving a portion of the stand on the ground, that which remains is destroyed or severely injured. The pure stands of balsam fir and the balsam fir and spruce stands in the Adirondack Mountains often suffer from wind alone a loss of one-tenth to one-fourth of the stand in a single season. On the other hand, the same species mixed with the deeper-rooted hardwoods suffer much less from windfall.

In a mixture of hemlock, hickory, and oak the roots of the hemlock occupy the surface horizons of soil. The other species are deep rooted and draw upon the deeper layers of soil for their moisture and nutrients to a far greater extent than hemlock. As they draw upon different soil horizons the mixture permits a more complete utilization of soil than is possible with a single species. Hartig first placed emphasis upon the importance of mixing deep-rooted species with shallow-rooted ones, in order to attain the best utilization of all layers of soil.

3. Tender species suffer less from frost, snow, and glaze when grown in mixture. Conifers as a rule suffer less mechanical damage from these causes when in mixture with broadleaved species. Other things being equal, the more irregular and uneven the canopy the less the damage. Trees in mixed stands vary in form and in rate of growth much more than those in pure stands, consequently the canopy is more irregular and uneven. A tender species in pure stands is fully exposed, particularly during its seedling stage in even-aged stands, and often suffers severe injury from frost. Many hardwoods, such as white oak, white ash, black cherry, and yellow poplar, are more or less sensitive to late spring frosts when young. They suffer much less when in mixture with more rapidly growing, thin-foliaged species like gray birch and black locust. Nisbet (1894) states that the technical value of the boles is less likely to be diminished by frost-shakes in mixed stands of conifers and broadleaved species than when the latter are grown by themselves.

4. Fungi and insects are less harmful in mixed stands. The best preventive measure against the occurrence and spread of epidemics in forests is the cultivation of mixed forest crops (Hartig, 1889). The destruction of natural mixed stands and the formation of pure, even-aged crops of a single species, have threatened forests in nearly all

countries where these practices have been followed. Extensive pure stands create conditions favorable for the rapid increase of destructive fungi and insects. European experience shows that the extensive pure forests of Scotch pine, Norway spruce, and other conifers made during the past century were damaged much more by insects and fungi than were mixed forests, and especially mixtures of conifers and hardwoods. On more than one occasion in central Europe the damage to pure stands by insects alone has reached the proportions of a national calamity. In Prussia and Saxony where 20 percent of beech or hornbeam is mixed with Scotch pine the resulting stand suffers but little from insect depredations at times when pure stands of Scotch pine suffer severely and in some instances are completely destroyed (Dunckleman, 1881).

Insect depredations in the pure, natural stands of ponderosa pine and lodgepole pine in the United States are much more severe than in any of the mixed stands so characteristic of forests of the eastern United States. Pure stands of black locust are, in most parts of the United States, likely to be completely destroyed by the locust borer (*Cyllene robiniae*) before they are 20 years old. The white pine weevil (*Pissodes strobi*) in southern New England not infrequently destroys the leader of every white pine in an even-aged plantation, but when in mixture with other species this species is usually damaged to a lesser degree. The number of insectivorous birds and other insect enemies is usually greater in mixed than in pure stands and they are thus better able to hold the insects in check. The extensive planting of white pine and other conifers in pure stands in New England and elsewhere in the United States will undoubtedly increase the danger of forest epidemics, the frequency of their occurrence, and the extent of their spread. As pointed out by Meinecke (1916) these dangers can be overcome only by better forest sanitation.

5. The fire danger is much greater in a stand of a single species, particularly if it be a conifer. The severity of surface fires which burn along the ground and do not get to the roots or into the tree crowns depends primarily upon the amount of dry material in a forest. However, the severity of a fire does not depend entirely upon the amount of dry material but also upon its character (Graves, 1911). Thus coniferous leaves that are dry and resinous make a quicker and hotter fire than hardwood leaves. Although a surface fire in a coniferous forest is usually hotter and more destructive than a similar fire in a hardwood forest, crown fires, which are far more destructive, are almost entirely confined to coniferous stands; sometimes, however, they occur in mixed stands of conifers and hardwoods. Crown fires spread with great

rapidity and often destroy vast areas of forest. Other things being equal, the rapidity of a crown fire and its intensity depend upon the character, density, and uniformity of the crowns. An even-aged coniferous stand of a single species such as white pine, Douglas fir, or hemlock provides the best conditions for a destructive crown fire. When broadleaved species such as birch, maple, and beech are mixed with conifers the danger from crown fires is less.

6. Mixed crops are more successful on poor sites than are most pure stands. Mixed crops maintain the quality of the soil much better than most kinds of pure crops. As a rule mixed crops do better on sites too poor for the same species in pure stands, because they draw upon different depths of soil and the species which compose them make different demands on the site. As a pure crop makes constant and unvarying demands on the site for its particular set of requirements, a soil naturally poor is likely to become deficient in moisture and nutrients. Often, however, it is more difficult to maintain a mixed stand on poor sites.

When attempts are made to grow exacting species like black walnut, black cherry, and white ash in pure stands, unless the soil is exceptionally fertile and well watered, they early begin to deteriorate, owing to the gradual deterioration and exhaustion of the soil. When the same species are mixed with beech, sugar maple, or other dense shade producers on the same quality of soil they succeed better because of the effect of the latter in gradually improving the soil.

On all except the best quality of forest soils the risk of soil exhaustion and deterioration by establishing a single species is far greater than when a variety of species is established in mixed stands. This is particularly true of thin-foliaged, intolerant species like many oaks, ashes, pines, and larches. When these species in pure stands have completed their principal height growth and demand increased growing space, the decrease in canopy and the reduction in number of stems per unit of area cause a greater exposure of soil to insolation and wind action, and thus decrease its quality and productive capacity.

From actual crop measurements made in Silesia, on soils similar in quality and conditions, the average annual increment in 80-year-old crops of pure Scotch pine was 18.3 cubic feet per acre, and of pure Norway spruce of similar age, 19.9 cubic feet (Nisbet, 1894). Mixed forests of the same age composed of Scotch pine, Norway spruce, and silver fir produced an annual increment of 23.5 cubic feet.

7. When early thinnings of a species in pure stands are of little economic value, more valuable thinnings may be realized by mixing

with it a species which brings better prices in small sizes. As a general rule cleanings and early thinnings from pure stands of softwoods are of little economic value. Hardwoods are more valuable for fuel and often can be utilized for this purpose, but there is usually no sale for softwoods of the same form and size. When species of approximately the same rapidity of height growth are grown together and early thinnings are necessary in order to overcome excessive crown and root competition between the principal crop trees and other species in the mixture, the other species should be removed. One of the economic advantages in the use of fillers in the artificial regeneration of forests arises when they have high value in small sizes as compared with the crop trees of the same size (Toumey and Korstian, 1942). They are gradually removed in thinnings.

8. Serious mistakes made in the selection of species for artificial regeneration are more easily corrected in mixed stands than in pure crops. When one or more of the species used in the formation of mixed stands are found unsuited to the site they can be removed in early cleanings and thinnings, leaving for the final crop only the species best adapted to the site. If, on the other hand, a single species is used which later is found to be unsuited for the site, the crop is a total failure and a new stand of another species must be established. When more than one species are used in regeneration, by adequate assistance in the way of tending the most desirable species in the mixture usually can be made to take a position naturally best suited for its growth and development. Without management, however, an inferior species in the mixture, through more rapid juvenile growth and denser canopy, may cause suppression and ultimate death of the superior species. When a single species used in regeneration is unable to conserve the general quality and productive capacity of the soil, owing to interruption of the canopy and decrease in number of stems per unit of area, under-planting is usually unavoidable when the canopy begins to break.

9. Mixed stands are usually more desirable from an aesthetic point of view than pure stands. Forests were first protected and improved by man for pleasure grounds and not for economic use. This idea still prevails in the management of many private woodlands throughout the country, particularly those in populated regions and in the vicinity of lakes and rivers that are favorable localities for summer homes. The operations concerned with the improvement of forests, from an aesthetic standpoint, deal with their adornment through operations that result in making them more beautiful and interesting. Among other things forest aesthetics takes cognizance of trees of striking and unusual form

and varieties with variously colored leaves, flowers, and fruit. A forest composed of a single species, paticularly if even-aged, is monotonous and unattractive compared with a mixed forest with its variety in color and form.

10. The natural regeneration of mixed stands is on the whole easier than the regeneration of pure crops. When an opening is made in a natural, mixed forest the ground is quickly reclothed with seedlings of the same species as those which formerly covered the area. The seedlings of various species in the mixture early begin to compete for space and light. By adequate attention and proper regulation of growth by means of cleanings, each species in the mixture can be developed in the proportion best fitted for superior silvicultural or economic results. With adequate attention there can be obtained for each kind of tree the soil and situation best adapted for it. Regeneration in small groups or patches is comparatively easy, much more so than when but one species occurs over the whole area with frequent changes in soil moisture and other site factors. When natural regeneration is mixed, danger to the young seedlings from fungi and insect pests is diminished. The danger of the entire reproduction being destroyed by frost, drought, or other climatic factors is much reduced.

European experience has fully demonstrated the great difficulty in obtaining natural reproduction under pure stands of Norway spruce and Scotch pine. When attempts are made to regenerate Norway spruce under pure stands of the same species by shelterwood cuttings, windfall is likely to occur. These trees, however, when in mixed stands, afford a better and more uniform natural regeneration.

The natural reproduction of pure coniferous stands, especially at northern latitudes, is often hindered by litter and unfavorable conditions of the soil surface. Frequently the best way to remedy this difficulty is by maintaining hardwoods in the conifer matrix, rather than by the use of fire, thinning, or other silvicultural treatment. Birch, beech, and alder serve this purpose in Europe. The advantages of mixed hardwood-conifer stands in providing leaf litter and soil conditions more favorable for forest reproduction and growth have been clearly shown for the white pine-hardwood region of New England (Fisher, 1928; Griffith, Hartwell, and Shaw, 1930).

11. A mixed stand is more easily transformed or modified to meet present or probable future demands of the market or to overcome a serious fungus or insect pest than is a pure stand. Not all species of trees command equally favorable market quotations for the products derived from them. In the management of a forest due consideration

must be given to the expectation value of the products when harvested. Not infrequently the relative value of the products from different species changes with time. Thus the hardwoods in many parts of the Adirondack Mountains once had little or no stumpage value. Today they are nearly as valuable as the conifers. It is possible to modify or transform a young mixed stand by favoring one species in the management at the expense of others. It has been relatively easy to transform the mixed hardwood forests of southern New England, composed of oak, hickory, and chestnut, to stands of oak and hickory, simply by the removal of the chestnut. The mixed stands of oak, hickory, and chestnut have not suffered irreparable loss through the death of the chestnut. Its removal has acted as a more or less severe thinning and has stimulated growth in the oak and hickory (Korstian and Stickel, 1927).

19. Even-aged Artificial Mixtures

Even-aged artificial mixtures are of great variety. In general, however, they may be reduced to three:

1. Sporadic — mixing by single trees.
2. Lines — mixing by alternate rows or strips.
3. Groups — mixing by clusters of trees.

Mixing by single trees requires the greatest judgment in selection of species for the mixture. In general, the height growth and natural pruning must be similar if all species are to do equally well. In practice, such mixtures are seldom successful because of the great difficulty in selecting species which behave in a similar manner in these two respects. The use of an equal number of all the species uniformly distributed can not be too strongly condemned for even-aged mixtures. However, the introduction sporadically of a limited number of trees of an especially valuable species, such as yellow poplar or ash, with the matrix species often can be done to advantage. The dependent trees should not be closer than at intervals of 20 to 30 feet. The species which forms the bulk of the crop as a rule must not exceed the dependent species in height growth, and, furthermore, it should be capable of pruning the dependent species. The greater value of the dependent species will usually more than compensate in money value for the less satisfactory growth of the predominant species. It should be clearly appreciated that the greater the number of species in the mixture, the greater is the uncertainty of the ultimate result on any particular site. The fact should also be emphasized that a mixture which may prove

valuable for one site may be a failure on another. The forming of complex even-aged mixtures should be avoided.

Mixing by lines is usually but little better than mixing by single trees, because of the same objections. The formation of mixtures by alternate rows, where it is expected that each will form a part of the ultimate stand, is usually unsuccessful. It is far safer to regenerate each species in strips of three rows or more, as each strip partakes more or less of the group character.

In most instances the formation of even-aged mixtures should be by groups, care being taken, however, that the groups are not so large that they partake of the characteristics of pure stands. Mixing by groups is most closely related to the method of natural reproduction in mixed stands. In such stands, as a rule, when a tree dies or is removed, a single species is dominant in seeding the open spot. Where several species start, one of them soon becomes dominant and crowds out the others, so that natural reproduction is usually more or less in the form of small patches of single species.

Regeneration in groups is not only the safest method of forming an even-aged mixture but is the one in which the varying character of the site can be utilized to the fullest extent. The size of the groups should vary with the site and the species. It is usually desirable that the groups be more or less variable in size and form, for it makes possible a better utilization of the site.

The permanent preservation of an even-aged mixture in suitable proportion becomes more difficult as the species differ in tolerance, height growth, suitability for the site, and form of the trees. Mixtures of tolerant species, such as sugar maple and beech, sugar maple and spruce, beech and hemlock, maple and white pine, are usually acceptable. Mixtures of tolerant with intolerant species permit great variety when suitable species are selected.

20. Two-aged Artificial Mixtures

When the maximum number of intolerant trees, such as larch, white oak, walnut, yellow poplar, cherry, or ash, is desired, they should be grown in two-aged mixtures, in the form of an overstory with a tolerant species in the understory beneath. The intolerant species should be regenerated some years in advance of the tolerant species. The time between the regeneration of the two age classes depends largely upon the species and the site. Thus European larch and sugar maple form an excellent two-aged mixture in southern New England. The regeneration is started as pure larch, and the maple is brought in 20 to 30 years

later, or when the stand becomes too broken to maintain an acceptable soil cover. Oak and hemlock, oak and sugar maple or beech, walnut and sugar maple, ash and beech are often found growing together under natural conditions and should form excellent two-aged mixed stands in artificial reproduction when the intolerant species are regenerated some years in advance of the tolerant species. Oak and beech are frequently grown in two-aged mixtures in Europe.

21. Temporary Mixtures

In some instances it is more advantageous for the mixture to be temporary, all but one species being removed before maturity of the crop. Such mixtures are useful when:

1. The rapid growth and high value of one or more species make it economically advantageous to remove them as thinnings, letting the remaining species form the final crop.
2. The original cost of seeding or planting can be materially reduced by the use of so-called fillers, that is, inexpensive species which serve to occupy a portion of the area but are removed in early thinnings.
3. A nurse crop must be provided to protect a tender species during its early life.

The chief reason for the use of fillers in planting operations is relative cheapness of the stock. In the use of fillers the expectation is that they will be overtopped and crowded out by the crop trees, taken out in early thinnings, or form a second story under the crop trees. The use of hardwoods as fillers in planting white pine in New England has not proved successful.

Much discussion has been given to the use of nurse trees in seeding and planting in this country. In most instances where nurse trees have been used the resulting stand has not been improved, but often, owing to rapid growth, shade-producing qualities, or abundance of nurse trees in the stand, the crop trees have been dwarfed, suppressed, or killed by them. Gray and paper birches, aspen, and similar light-foliaged species, which make rapid juvenile growth but do not attain large size, are most acceptable as nurse trees. Advantage can often be taken of a natural nurse crop in artificial regeneration. It is imperative, however, that the nurse crop be not too dense, or the crop trees beneath it will not thrive. Tolerant species can withstand a denser nurse than intolerant. The nurse crop, as a rule, should be established a number of years in advance of the tender species. It should be hardy, grow rapidly, have open foliage, and should be removed when the crop trees are no longer benefited by it.

22. DIFFERENTIATION OF STANDS ON BASIS OF DENSITY

Density relates to the relative closeness of trees in the stand. Closeness may refer to nearness of the crowns, boles, or roots; usually, however, it refers to closeness of the crowns.

Laymen look upon the restricted space which trees in a newly regenerated natural stand are given, and the closeness of individuals in artificial regeneration, as an extravagance. It is contemplated, however, by foresters, that no tree shall take on an "aesthetic form" and stand alone but that all shall stand sufficiently close to develop a continuous canopy under which the lower branches will die before they become sufficiently large to affect seriously the quality of the wood. This is attained by establishing a thousand or more trees on an area where a hundred or less will be brought to maturity. The silvicultural explanation of this operation is to be sought in the individual tendency of some trees to make more rapid growth than others. In succeeding cleanings and thinnings the better trees are given ample space.

In a stand mixed by individuals, growth develops naturally and most rapidly when the mixture gives to each individual its necessary soil space. When one or more species in the mixture do not retain their necessary soil space they are likely to be eliminated from the stand.

23. Crown Closure

The theory and appreciation of crown closure are very important in forestry. The skill of foresters was directed early toward the retaining of a closed canopy throughout the entire life of a stand. More recently the tendency has been more and more toward the practice of adhering to a more open development of crowns during the second half of the life of a stand. The prevailing opinion at present is that from a determined age onward, full crown cover is injurious to the soil and restricts growth. Formerly the maintenance of a closed crown cover was considered the end of all stand improvement work. Regeneration was established closely spaced in order to hasten the formation of a closed canopy. An overly dense stand of reproduction, however, causes stagnation in growth as soon as complete crown cover is obtained. Crown closure is attained earlier with rapidly growing species and on good soil.

24. Degree of Crown Density in Stands. — The degree of crown density in stands is usually expressed numerically on a scale of 1.0 to

0.1. Thus a density of 1.0 implies that there are no openings between the crowns, a condition rarely, if ever, found in forests of temperate and cold regions. A density of 0.1 implies that openings between the crowns are 90 percent of the total area and only 10 percent is occupied by the crowns.

Much research has been devoted to efforts to grade crown density and find an accurate numerical expression, and thereby a convenient means to interpret and control the grades of density of different species, and combinations of species for different sites. Such an expression would be of great value to silviculturists in opening up stands, but an acceptable measure has not yet been found. Mayr (1925) is inclined to rejoice over our inability to establish an accurate numerical measure of density. He believes that the employment of a fixed measure would lead to the falling off in silvicultural observations and to serious mistakes.

The degrees of crown density are relatively expressed in the following terms:

Closed. When crowns form an uninterrupted cover and permit little or no light to reach the ground.

Dense. When three-fourths or more of the ground is shaded by crowns.

Thin. When between three-fourths and one half of the ground is shaded.

Open. When less than one-half of the ground is shaded by crowns and when the shade is not in isolated patches.

Park-like forest. When the shade occurs only in isolated patches.

Crown closure is most complete when the crowns come together, over and beneath each other. This is illustrated in stands of tolerant species of all sizes and in other stands in the thicket or pole stages. The crowns are usually considered closed when those beneath become weak. The densest crown closure of intolerant species like white oak and larch is in the thicket stage; and the densest crown closure of tolerant species, as beech, sugar maple, and spruce, is at the stage when the trees are well on toward maturity.

As crown density is expressed in terms of light and shade on the forest floor, efforts have been made to determine the degree of density of different kinds and types of forest by measuring the intensity of light that reaches the forest floor through the canopy. Such studies have been made by many research workers, but they are seldom employed by practicing foresters because of the great difficulty in the assessment of the crown cover by their application.

25. Conditions Which Influence Crown Density. — The density of canopy is influenced by a large number of conditions and circumstances, among which the following are of special note:

1. *Manner of formation of the stand.* The densest stand, while young, is obtained from natural and artificial seeding which results in complete reproduction. The stands that result from planting are usually more open when young. Stands from closely spaced planting close early, whereas delay in closing is prolonged by increasing the spacing distance.

2. *Quality of the soil.* Crown cover is denser and remains uninterrupted longer on good soils than on poor soils. Poor soils, however, carry a large number of trees in the same age classes.

3. *Lack of uniformity in moisture and temperature conditions of air and soil.* When two sites are similar in moisture conditions of air and soil and have adequate moisture, the warmer site sustains a forest having the denser canopy. The crown cover is much more open in cold regions. Nansen (1914) explains the wide spacing of trees in the forests of northern Siberia as due to the wide spread of surface roots over a shallow soil resting upon soil perpetually frozen. When two sites are alike in air temperature and there is deficient available moisture, the drier one has the more open crown cover. Thus the park-like forest of the woodland cover types in the southwestern United States, where the trees are short and isolated, is explained in the small amount of available moisture in the air and soil.

4. *Differences in species.* Although species in themselves seldom determine the density of crown cover, intolerant species generally develop an open crown density in early life, intermediate species generally hold their crown density for a longer time than intolerant ones, and tolerant species usually hold their crown density throughout life.

26. Importance of Crown Closure and Its Influence on Life of a Stand. — Maximum height growth in all stands in the pole and young timber stages is attained under side pressure from competing individuals. Exercise of the best practice in opening up a stand through interference with its natural development so as to favor one species or certain trees in a stand to the disadvantage of others is a large part of the entire field of silvicultural practice.

The importance of crown closure in its bearing upon the development of stands can scarcely be overstated. The best use of the area is that which gives the greatest number per acre of thrifty trees of the most desirable species. This number necessarily varies with the age and size of individuals, the species, and expanse of crown. In selection

forests it is not so much number of trees per acre as expanse of crown of the older age class that accounts for full crown cover. For this reason in most virgin forests the crown cover is chiefly formed by a small number of large widespreading individuals. Thus in some of the virgin stands of beech, yellow birch, and sugar maple in New England and New York, the crown cover is chiefly composed of the widespreading crowns of trees in the upper age class. The subordinate classes produce a very small part of the crown cover although they may outnumber the older age class of dominant trees ten to one.

In a stand that has been intelligently thinned at intervals during its development, there are many more trees in the class that accounts for full crown cover and there is a much smaller number in the subordinate classes. In even-aged stands, competition, soon after the stand closes, differentiates the trees into classes, based on degree of dominance. With the natural development of the stand some individuals forge ahead but more and more fall behind each year. When well on toward maturity there is a comparatively small number of dominant individuals which account for full crown cover, although a larger number than in the selection forest. When an even-aged stand is systematically thinned so that each remaining tree has adequate soil space and is reasonably crowded from the side, the maximum number of individuals accounts for full crown cover. The restriction of growing space necessarily restricts the diameter of the crown and modifies its form. Thus when red spruce is crowded from the side but exposed to overhead light the diameter of the crown becomes restricted and its form modified. When an individual of this species maintains itself under the canopy of an overstory, it flattens its crown. It assumes the "umbrella type" of crown so characteristic of oppressed red spruce in the Adirondack Mountains.

Shortening of the crown in proportion to total height of tree usually begins with the clearing of the bole of limbs. The crown, however, continues to lengthen from above. Both tolerant and intolerant species, when standing alone, lengthen their lower branches, which results in the progressive widening of the crown and retaining of branches to the base. The lower branches by their longer growth extend out beyond the higher branches. When trees are brought together in stands and the growing space restricted, the widening of crowns is no longer possible, the branches stand directly over each other, and the lower ones die. These conditions are most completely realized when tolerant species develop in pure stands, as sugar maple, beech, and red spruce. They are most incompletely realized in intolerant mixtures. The competi-

tion is most intense in pure, even-aged stands of very tolerant species when all the individuals react similarly. The greater the variation in soil conditions the less intense the contest. A pure, artificial stand of white pine grown on best quality soil and prepared by plowing and harrowing exhibits intense competition shortly after the canopy closes. The trees are so nearly uniform in size and vigor that they all suffer alike from competition, and, if thinning is not immediately undertaken to relieve the tension, the entire stand is weakened and the growth declines. It is inferior to a similar stand on a poorer, uncultivated soil, where differentiation into crown classes began early and where dominance is expressed at once. In mixed, uneven-aged stands, competition is between species and individuals which do not react similarly. When to the differences in age of individuals and in soil are added the differences in species, the question of dominance is more quickly determined. The slower-growing species fall behind and form gaps in the canopy into which crowns of the more rapidly growing ones extend, eliminating by their expansion all intolerant laggards. If tolerant they spread out and form a more or less permanent understory or later grow up into or through the crown cover, often eliminating it in turn. Thus in natural, even-aged stands of paper birch and white spruce in Canada the spruce at first falls behind, giving more crown space to the birch; later, however, the spruce grows up through the birch canopy which soon becomes broken and destroyed.

When intolerant and tolerant species are mixed stemwise or individually, the intolerant species develop clean stems, the tolerant less clean. When a stand is so open that it permits the entrance of intolerant species, the natural pruning of all boles is unsatisfactory; although the lower limbs remain alive they function but little and thus do not add to the growth of a stand during the latter part of its silvicultural development.

27. **Crown Closure and Growth.** — Growth progressively increases up to the time the crowns begin to die from below. Height growth, however, increases with a moderate crowding of side branches following closing of the crowns, but crowding reduces diameter growth. The regulation of density becomes a forester's means for developing a bole form which approaches, to a greater or less degree, that of a cylinder. It is not the trees on the border of a stand, which enjoy the greatest soil space and most soil nutrients, that have the greatest height growth. The greatest height growth is in the interior of a stand, when the crowns are moderately crowded from all sides and the greatest diameter growth is on the border.

Because crown closure and crowding from the side increase natural pruning and length of the bole and reduce diameter growth and render it more uniform, they profoundly affect the character and quality of the wood. Although trees developed in closed stands, but with thinnings sufficiently frequent to give each crop tree adequate crown space, produce wood of the highest quality, the combined growth per unit of area is usually no greater than that of a smaller number of crop trees with equivalent crown density.

The beginning of seed production is usually much delayed through crown closure. Not only is the beginning of seed production in most species some 10 to 30 years later than when the same species is growing as free-standing individuals, but the resting period between full seed years is much longer. Delayed seed bearing in dense stands is due to inadequate reserve food materials. Reduced crown and root space inhibits accumulation of adequate elaborated food, and after that required for vegetative growth is consumed there is little or none left for seed production.

28. Crown Closure and Soil Quality. — The preservation of quality of soil is not the best under the thickest crown cover of tolerant species. Under such a cover, raw humus is likely to appear and the soil may become acid in character, and deficient in air and heat. So also, under the incomplete cover of intolerant species and under wide-spaced tolerant trees, the preservation of soil quality is not the best. This is due to overly rapid decomposition of litter and the development of forest weeds. Satisfactory decomposition of litter is usually at its best in virgin forests. Artificial stands have a less satisfactory crown cover in that they are likely to be too dense or too open. They do not equal natural forests in accumulation of nutrients in the soil. The crown cover of a pure stand is usually much poorer in this respect than that of a mixed stand.

29. Crown Classification

Trees in a stand are commonly classified on the basis of crown position. Species, age, and competition are the most influential factors in determining the position of the crown in an uneven-aged stand. In pure, even-aged stands, competition is generally the most significant factor.

30. Crown Classification for Even-aged Stands. — The most commonly accepted scheme for the classification of living trees in even-aged stands in the United States is the relatively simple one adopted by

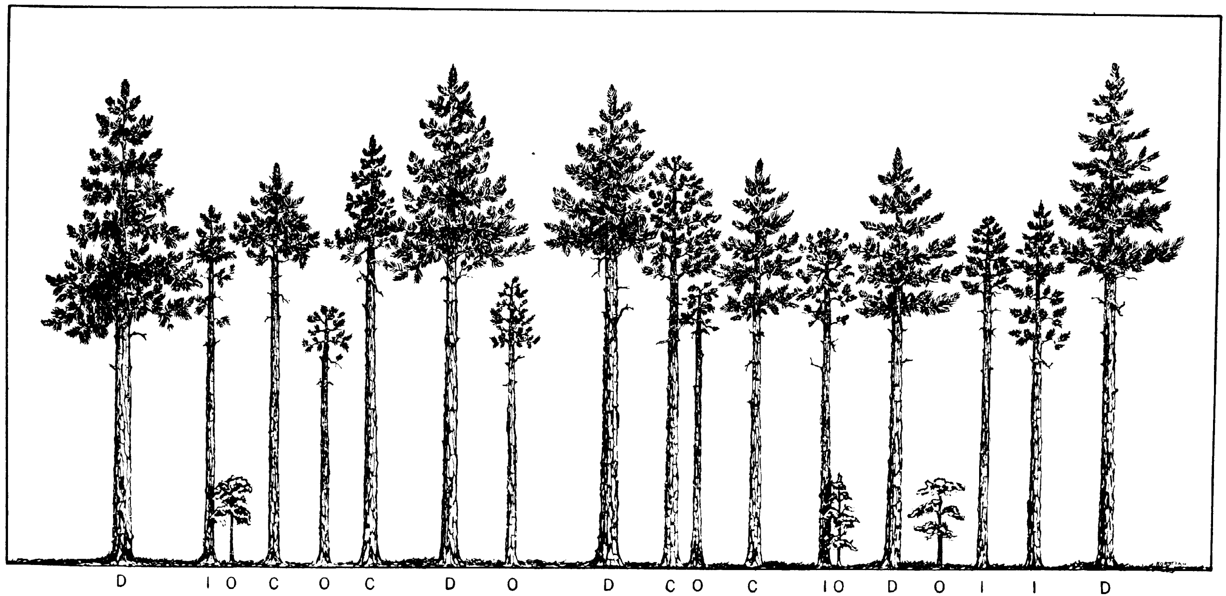


FIG. 17. — Diagrammatic representation of a transect through a 33-year-old, even-aged stand of loblolly pine showing crown classes: *D*. dominant; *C*. codominant; *I*. intermediate; *O*. overtopped. Based on actual measurements of total height, crown length, and d.b.h. The three shortest understory trees are hardwoods.

the Society of American Foresters (1944). In this scheme the following crown classes (Fig. 17) are usually distinguished:

Dominant. Trees with crowns extending above the general level of the crown cover and receiving full light from above and partly from the side; larger than the average trees in the stand, with crowns well-developed but possibly somewhat crowded on the sides.

Codominant. Trees with crowns forming the general level of the crown cover and receiving full light from above but comparatively little from the sides; usually with medium-sized crowns more or less crowded on the sides.

Intermediate. Trees shorter than those in the two preceding classes, but with crowns extending into the crown cover formed by codominant and dominant trees; receiving a little direct light from above but none from the sides; usually with small crowns considerably crowded on the sides.

Overtopped. Trees with crowns entirely below the general level of the crown cover, receiving no direct light either from above or from the sides. These may be further divided into *oppressed,* usually with small, poorly developed crowns, still alive, and possibly able to recover; and *suppressed,* or dying. The term *suppressed* implies a physiological response. It should be applied to the overtopped trees in a stand that make little or no recovery after the surrounding trees have been removed. The term *oppressed* should be applied to the overtopped trees that respond after opening the stand.

The differentiation of the stand into the above classes is simplest and easiest in an even-aged forest of a single species.

31. Dunning's System of Crown Classification for Uneven-aged Stands. — The above system of classification is generally unsatisfactory for uneven-aged stands. When a stand is all-aged, mixed, and composed of trees of varying degrees of tolerance, certain species may stand under the crowns of others and still not be suppressed so far as their growth and persistence in the stand are concerned.

For stands of uneven-aged ponderosa pine in California, Dunning (1928) developed a system in which trees with certain combinations of characteristics that are known to have similar influences on growth and seed production are grouped into classes. The major factors involved in the segregation of these classes are:

1. Four general age groups — young (less than 50 years), thrifty mature (50 to 150 years), mature (150 to 300 years), and overmature (over 300 years).

2. Degree of dominance within these age groups, expressed in terms

of conventional crown classes — isolated, dominant, codominant, intermediate, and overtopped.

3. Crown development.

4. A supplementary estimate of thrift designated in three degrees of vigor — good, moderate, and poor.

In this scheme Dunning recognizes seven tree classes (see Fig. 18) as follows:

Class 1: *Age class*, young or thrifty mature; *position*, isolated or dominant (rarely codominant); *crown length*, 65 percent or more of

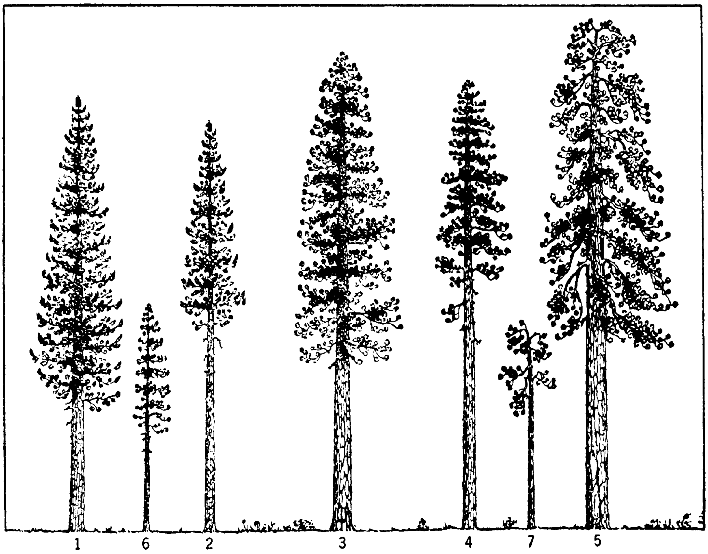


Fig. 18. — The 7 tree classes recognized in Dunning's classification for uneven-aged ponderosa pine. (*After Dunning, 1928.*)

the total height; *crown width*, average or wider; *form of top*, pointed; *vigor*, good.

Class 2: *Age class*, young or thrifty mature; *position*, usually codominant (rarely isolated or dominant); *crown length*, less than 65 percent of the total height; *crown width*, average or narrower; *form of top*, pointed; *vigor*, good or moderate.

Class 3: *Age class*, mature; *position*, isolated or dominant (rarely codominant); *crown length*, 65 percent or more of total height; *crown width*, average or wider; *form of top*, round; *vigor*, moderate.

Class 4: *Age class*, mature; *position*, usually codominant (rarely isolated or dominant); *crown length*, less than 65 percent of the total height; *crown width*, average or narrower; *form of top*, round; *vigor*, moderate or poor.

Class 5: *Age class*, overmature; *position*, isolated or dominant (rarely codominant); *crown* of any size; *form of top*, flat; *vigor*, poor.

Class 6: *Age class*, young or thrifty mature; *position*, intermediate or overtopped; *crown* of any size, usually small; *form of top*, round or pointed; *vigor*, moderate or poor.

Class 7: *Age class*, mature or overmature; *position*, intermediate or overtopped; *crown* of any size, usually small; *form of top*, flat; *vigor*, poor.

Since this system of classification correlates vigor, age class as broadly determined, and seed production with external appearances of the trees of each class, it is likely to become a model for schemes for other species elsewhere.

A somewhat similar but more detailed system of classification for uneven-aged stands of ponderosa pine, which is particularly useful in classifying trees of this species from the standpoint of susceptibility to barkbeetles, has been developed by Keen (1936, 1943). It comprises 16 classes based on 4 age groups (stages of maturity) and 4 crown vigor groups (determined by crown size, dominance, and thrift). Other classifications have been prepared for ponderosa pine in the Black Hills by Hornibrook (1939), for this species in the Southwest by Thomson (1940), and for lodgepole pine in Colorado and Wyoming by Taylor (1937).

32. Root Closure

As the portions of a stand above ground, namely, the shoots, begin to develop and spread out, exposing the crowns to light, the portions below ground, namely, the roots, begin to develop and spread out, exposing their surface to a progressively larger body of soil. The portions above ground develop a canopy under normal conditions, more or less even and raised to a varying distance above the soil. The portions below ground develop a more or less continuous root system under normal conditions at varying distances below the surface, which may be likened to the canopy above ground.

Under average conditions of available moisture the lateral expanse of roots below ground is much greater than the lateral expanse of branches above ground. This is particularly true in the seedling, thicket, and pole stages in the life of a stand. The vertical extension

of crowns above ground always has much greater magnitude than the vertical extension of roots below ground. When in closed stands, the boles of trees progressively raise the branch systems higher and higher above ground until height growth is attained. The root systems of trees, no matter how dense the stand, are not progressively extended downward into the soil. The interwoven mass of roots is most dense in the uppermost layers of soil. The greater proportion of roots in most forests, no matter how old and large the trees, is in the uppermost three feet of soil.

The roots do not spread out evenly in all directions from the base of the bole; therefore all parts of the soil are not equally occupied by roots. The unoccupied and least occupied portions retain more moisture during periods of drought and have more available soil nutrients. Seedlings arising from seed which fall upon these places and germinate have a better chance to become established than those from seed falling upon soil already fully occupied by tree roots. The uneven distribution of reproduction in a stand may be due more to the irregularities in distribution of the root systems than to openings in the crown canopy.

33. **Effect of Root Closure on Life of a Stand.** — When a stand is so dense that the root systems occupy the upper soil horizons so completely that little or no unoccupied space is available (comparable with full density above ground), the roots overlap and the closing below ground may be as unfavorable as too great a density of crown cover above ground. On the other hand, on sites with little available soil moisture unfavorableness is chiefly expressed in overcrowding below ground. On such sites crown density may be open with each tree standing free, but at the same time root density is full, with a more or less continuously interwoven mass of roots. The more arid the site the greater the competition for available soil moisture and the more completely is competition transferred from crown to roots. Competition for crown space decreases and competition for root space increases. Stands exhibiting great density in the parts above ground and having the most complete crown cover are those of humid regions, growing on deep, moist, fertile soils. Stands characteristic of regions with scanty or inadequate precipitation, and on thin, poor soils, are usually open so far as the crowns are concerned, but in their climax form are closed from the standpoint of root space. Thus the ponderosa pine forests of northern Arizona and New Mexico have more or less wide-spaced crowns which permit a large amount of sunlight to reach the forest floor. The soil, on the other hand, is more or less fully occupied; consequently other individuals can not enter except in soil not already completely

occupied by roots. Reproduction is very irregular and is distributed entirely without relation to crown density. Its distribution is determined by competition for available soil space and not competition for crown space. Frequently when a climax stand is composed of individuals that, so far as the parts above ground are concerned, are free standing and open, it is closed in an ecological sense, in that other individuals are unable to enter without the removal of some of those already there. The stand is closed from the standpoint of root space.

34. Conditions which Influence Density of Boles

The number of boles per unit of area is not directly correlated with the density of crown cover. In other words, a 100-year-old stand of sugar maple or beech with full crown density, for example, has a different number of boles per unit of area than a 100-year-old stand of white pine or red spruce of similar crown density. Within a species, the number of boles per unit of area is first of all determined by their age and its effect on size. Thus in an even-aged stand of white pine as many as 2,500,000 separate stems per acre will not overcrowd the stand during the first 2 years following germination. This number will be reduced to 50,000 to 75,000 by the end of 5 years; 6,000 to 12,000 by the end of 10 years; 1,200 to 2,400 by the end of 20 years and to 500 to 1,000 at the end of 40 years, depending on the quality of site. Although size is the greatest factor in determining number of boles per unit of area, the cross-sectional area of the crown is more important than the cross-sectional area of the bole. Species with long narrow crowns like spruce form stands having not only a large number of stems but a larger basal area per unit of forest area than yellow birch and beech, which become wide crowned as they approach maturity.

Although there is a rapid decrease in number of boles per unit of area in the development of an even-aged stand, the basal area[1] gradually increases rather than decreases with the reduction in the number of stems. For example, in a fully stocked stand of white pine at 25 years of age the basal area per acre in southern New Hampshire is 150 to 190 square feet; at 35 years, 175 to 230 square feet; at 45 years, 190 to 240 square feet; at 55 years, 200 to 250 square feet; at 65 years, 210 to 255 square feet, and at 85 years, 220 to 265 square feet, depending on the

[1] Basal area is the area of a cross section of a tree, usually expressed in square feet and usually referring to the section at breast height. The sum of the basal areas of trees in a stand is the basal area of the stand and is usually expressed in square feet per acre.

quality of site (Graves and Ziegler, 1910). In a 50-year-old white pine stand with full crown density, the basal area is from about $\frac{1}{3}$ percent to nearly $\frac{1}{2}$ percent of the total land area.

Bole density is not only an important factor in determining clearness of bole, its form and taper, but also in determining position of the growing center in its cross-sectional area. As a rule the mechanical and physiological centers of the bole fall together in a tree standing in the open. On the other hand, owing to the unsymmetrical development of crown and roots, the physiological center of a tree growing in a stand does not always correspond with the mechanical center; the radii are more or less unequal.

35. DEVELOPMENT OF STANDS

The various changes that take place in a stand throughout its duration of life are considered under development. The development of a stand is different from the development of an individual tree. The most striking characteristic in the development of stands is the gradual but remarkable decrease with age and size in number of individuals occupying a definite area, as is best illustrated in an even-aged stand of a single species. The differences in the development of one stand, as compared with another, depends upon both inherent and external characteristics. Development varies with species and with the nature and quality of site.

36. Development of Even-aged Stands

All even-aged stands pass through certain distinct stages of development and undergo certain changes. These may best be described by reference to a specific case. Suppose that a plantation of white pine has been established with the trees set 6 feet apart. The first stage in its development is the period during which the trees stand entirely isolated. Each has full space for the development of crowns and roots. The crowns reach to the ground and each tree grows as if there were no other trees near it. After a few years the crowns expand so much that they touch each other. This is the beginning of the second stage. Because of the side shade and physical interference of the crowns there is a restriction in their side development and the competition for growing space begins. Competition is greater on good sites than on poor sites. The meeting of the crowns constitutes the beginning of the formation of the canopy. The canopy is formed sooner and the tree classes are more sharply separated on good sites than on poor sites. The forest floor is then more or less shaded. The lower branches of the trees begin

to die, signifying the beginning of natural pruning. The litter begins to accumulate on the forest floor, and true forest conditions are established in which the trees react on each other to their mutual help or injury, as the case may be.

One of the first results of the competition between trees is their separation into crown classes. The most rapidly growing individuals become the dominant trees; the weakest trees are soon crowded and become overtopped; the others are in the intermediate classes. As stands develop, competition becomes more and more intense. As the requirements of trees for crown space increase, the differences between the crown classes become greater. Many suppressed trees die; many trees which at first are intermediate become overtopped; some of those which at first are barely intermediate fall into the lower intermediate class; and some dominant trees drop into the codominant class.

During the second stage in a stand's life the canopy is rising steadily above the forest floor as the trees grow in height and as natural pruning proceeds. At first the canopy is equivalent to the height of the trees and practically reaches the ground. As the trees grow taller it represents progressively a smaller proportion of their total height. In youth the crowns of the trees touch only near their bases. As they grow and expand, the point of mutual contact comprises nearly the whole length of the crowns. During this period the reduction in number of individuals by suppression and death is more rapid than later on; the principal growth in height takes place; the density of the canopy, particularly in intolerant and partly tolerant trees, reaches its maximum and casts the heaviest shade. Natural pruning is at its best.

During the third period the stand continues strong and vigorous and the canopy remains intact, particularly in tolerant species. Natural pruning continues, though less rapidly than previously, and there is still a gradual reduction in number of trees per unit of area. Wood clear of knots is produced. The trees have already acquired their height. At the beginning of this period the trees are large enough for many commercial purposes and, as they increase in size, they progressively advance to sizes and grades which have a higher value per unit of measure. There is, therefore, an increase in the value of the stand from year to year, not only due to its increase in volume but chiefly due to the progressive improvement in the quality of product. This improvement in quality is called quality increment and takes place chiefly during the third period of a stand's life.

The appearance of marked openings in the canopy indicates the end of the third stage of a stand's life and the beginning of the fourth period,

or period of retrogression. The beginning of this period marks the real silvicultural maturity of a stand. Many individuals are able to live on for many years, remaining sound and increasing in value with every year. The stand is, however, mature, for its integrity as a completely even-aged stand is lost and it steadily deteriorates. There is a gradual reduction in vigor of the trees. The crowns open up, the density of foliage is diminished, and the rate of growth of individuals is lessened. Time begins to tell on the trees, injuries from storms and from other causes are evident. The trees become more susceptible to disease and eventually a tree dies here and another there. Breaks in the canopy occur in this way. Reproduction of trees, shrubs, grass, and other herbage begins to appear in openings. The loss resulting from the death of occasional trees offsets or may be greater than current increment, and the stand is losing rather than gaining in economic value or in increment or in both. In any event, the forest becomes more and more broken and, as new growth takes its place as a part of the stand, there follows an irregular, uneven-aged form of forest. If it is left entirely undisturbed the species originally occupying the ground will come in and succession will ultimately lead to the climax type for the site.

The beginning of the establishment of forest conditions, the rapidity of differentiation of crown classes, the rate of reduction in number of trees, the period of maximum density, the time of maturity all differ with different species. For example, an even-aged stand of an intolerant species like ponderosa pine has a development different from that of red spruce. The periods are reached at different ages and the various changes in the stand occur differently, because of the difference in tolerance and other silvical characteristics of the species. If a stand is established by natural reproduction rather than by planting, usually the trees differ somewhat in age, often 10 to 20 years. As a result, the stand is not as uniform, the trees do not come together as regularly, there are likely to be some groups forming a canopy earlier than others, the spacing is less regular, some parts are denser than others, the reduction in number of trees is less regular, and the forest canopy is less uniform.

If the trees are very close together, their crowns meet earlier than when there are fewer trees in the stand. The trees may be so close together that the differentiation into crown classes is retarded and both height and diameter growth are checked. Overcrowding an even-aged stand may result in reducing the canopy to such a thin layer that the stand as a whole cannot thrive.

37. Development of Uneven-aged Stands

The development of an uneven-aged stand does not present separate life stages, as in even-aged stands. The form is irregular and there are mingled together trees of many ages and sizes; a complete canopy is formed by the closure and overlapping of the crowns. When a stand is mixed and of tolerant species the mingling of the age classes is promiscuous. Single trees of different ages are mixed together though frequently there are small groups of a single age class. Where an old tree dies the young trees that stand beneath it are released. The most rapidly growing species take the lead. If the slower-growing trees are tolerant, they may be laggards in the stand without much danger of death. Stands of tolerant species have a two or more storied condition, a deeper canopy, and a greater real density. Competition for crown and root space is less intense when a stand is mixed because there is more growing space for both, as each species seeks a different level. The deeper canopy prolongs the period of maximum density, a greater number of trees grow per acre, and the increment is consequently greater. In pure stands, the trees have a more uniform rate of growth, more uniform crown development, the same depth of roots, and the same demands on soil moisture and nutrients. Species in mixture may differ in some or all of the above respects.

When several species grow together in an uneven-aged stand the forest becomes very complex. There is a constant shifting about of the species from point to point as trees die and are replaced by others. Although an entire stand may remain stable in composition, form, and yield, a single acre may undergo changes in one direction or another with reference to the arrangement and abundance of each of the several species. When an opening is made by the death of an old tree or group of trees, all species adapted to the site contend for its control. Which species wins in the competition depends on a great variety of conditions and circumstances. Reproduction is continually taking place. Such a forest of tolerant species gives the impression of very great density. If the species are intolerant, the age classes tend to occur in groups. Reproduction takes place only when an opening is large enough to admit the requisite amount of light and provide adequate root space. The number of small trees is less than in stands of tolerant species and the total number of trees per acre is less.

There is neither gain nor loss of increment in a virgin all-aged stand. The loss by death is balanced by the increase in growth of the living trees. After an interval of a century there would be the same amount

of timber standing, the same species of trees, the same form of stand, and the same processes of life, growth, death, and reproduction. Tolerant species have a great advantage in an all-aged stand because they start in the shade and persist until there are openings from one cause or another which are large enough to aid their development. Intolerant species, on the other hand, require a substantial opening for reproduction. In the struggle for existence tolerant species sometimes gain the upper hand and exclude intolerant species entirely from certain sites. Thus in certain areas in Pennsylvania, hemlock grows in pure stands, having successfully crowded out the less tolerant white pine and hardwoods.

It might be inferred that a climax forest would always be composed of the most tolerant species adapted to the site. This would be the case in forests if no openings occurred, large enough for intolerant trees to obtain a foothold. There are, however, always certain forces in operation which sooner or later cause large openings. Windfall, windbreakage, glaze damage, lightning, diseases, and insects are operating to some extent in all forests. Where openings are made by these causes, the intolerant species have an opportunity for reproduction.

It is often the species with the greatest vigor of reproduction which succeeds in occupying an opening. Intolerant species frequently have a more rapid height growth in early life. After germination they are able to out-distance their more tolerant competitors and thus maintain their position. Compare, for example, the early rate of growth of the intolerant tamarack and the intermediately tolerant white pine with the tolerant spruce, hemlock, and fir.

Tolerant trees which start in deep shade often pass through a long period of oppression. Red spruce sometimes remains a small oppressed tree, for 75 years, with a short, flattened umbrella-shaped crown. This species has a remarkable power of recuperation and even after a half century or longer, during which it has persisted as an overtopped tree, it may grow and develop into a valuable tree when released. When released this species lives longer and continues at a better rate of growth than trees that have never been oppressed. Hemlock and white pine when released after a long period of oppression exhibit the same reactions.

The crown classes are much less regular and less easily distinguished in an uneven-aged stand than in an even-aged stand. In an uneven-aged stand, some trees are beneath the main canopy; yet they are thrifty and promising and therefore not suppressed. The individual trees in uneven-aged stands grow less regularly than in even-aged

stands. Trees of the same age show a greater variation in size, in crown development, in natural pruning, and in quality of product. There are also greater periodic variations in growth. The cross section of a tree from an uneven-aged stand is more likely to show periods of slow and of rapid growth.

38. Development of Sprout Stands

The development of sprout stands differs from that of stands from seedlings. The young sprouts grow so rapidly that a canopy is formed sooner than with trees that start from seed. As the trees occur in clumps, there is vigorous competition among members of a single clump, which causes the individuals to assume characteristic forms. If the clumps are close together, there is a dense canopy. In a sprout stand the period of maximum density occurs earlier than in a seedling stand because the trees reach their maximum vigor relatively early. The silvicultural maturity is also early. Many individuals infected by disease from the old stump die when relatively young. A stand of oak sprouts reaches its silvicultural maturity in southern New England when 60 to 80 years old, or at less than half the age of oak stands originating from seed.

CHAPTER XV

REPRODUCTION, GROWTH, AND YIELD OF STANDS

1. REPRODUCTION OF STANDS

The reproduction of a stand may arise in one or another of the following ways:

1. Naturally, that is, from self-sown seed or otherwise through natural agencies. In such cases the reproduction is distinguished as natural.
2. Artificially, that is, from seed or plants brought to the site by man. The reproduction is then distinguished as artificial.
3. Through a combination of natural and artificial means. The reproduction is distinguished as mixed.

2. Natural Reproduction

A stand reproduces itself without the assistance of man under the following three conditions:

1. Suitable conditions for seed production.
2. Suitable soil conditions for reception and germination of seeds and survival of seedlings.
3. Both light space and soil space for growth and development of young plants.

In a virgin forest, as the trees mature, die, and fall to the ground, their places are taken by younger trees. Reproduction takes place in more or less isolated patches where trees have fallen, thus providing both light space and soil space. A typical virgin forest in its climax form contains trees of all ages. It is fully stocked at all times, unless disturbed by fire, insects, or other external agents which cause the destruction of all, or a large number, of the trees at one time. In such a forest natural reproduction is easily attained. The small openings caused by the death of a tree here and there are surrounded by seed trees, and the soil is in excellent condition for germination of seed. Both light space and soil space stimulate rapid growth in seedlings. Thousands of seedlings fill every opening and early begin adjustment for space. When a virgin forest is disturbed by some external agent which destroys a large number of trees at one time, or all the trees over considerable areas, conditions often arise which make natural regeneration very slow and difficult. Some openings are so large that insufficient

seed is brought to the open spaces from the surrounding trees. More and more seed is brought in with succeeding years but inadequate seed supply and long exposure of soil to the sun and wind result in fragmentary and incomplete reproduction. One hundred or more years are sometimes necessary to bring forests back to a fully stocked condition.

3. Origin of Natural Reproduction. — In virgin forests reproduction originates from the following sources:

1. Seeds.
2. Stool shoots.
3. Natural layering.
4. Suckers.
5. Detached vegetative parts.

Reproduction of forest trees is chiefly from seeds. In only comparatively few species does it arise from stool shoots, natural layers, and suckers. Reproduction from stool shoots of oak, chestnut, and basswood among hardwoods and redwood among conifers is very frequent, following fire and other damage. Reproduction of balsam fir and mulberry sometimes arises by natural layering, whereas beech and black locust often reproduce from root suckers. Reproduction of certain willows and species of *Opuntia* is, to some extent, from naturally detached vegetative parts.

4. Conditions Under which Natural Reproduction Can Not Be Attained. — There are ordinarily but two conditions of site which make natural reproduction impossible:

1. Areas where seed trees are too remote or too few to provide adequate seed, or where the seed is destroyed by rodents or other agencies.
2. Areas where seeds will not germinate or young plants become established, owing to unfavorable site conditions.

Natural regeneration is usually possible under all other conditions, and the question of its employment in preference to artificial regeneration is entirely a matter of economics.

As soon as a natural forest is interfered with by man in order to make it of greater economic value; as soon as it is changed from a wild stand to a managed stand, and the more it loses its mixed, uneven-aged character, the more uncertain and fragmentary is natural reproduction. The more nearly cultivated or managed stands approach natural stands the more certain is reproduction when left to natural agencies. All silvicultural operations develop more or less unnatural conditions, and in attempts to attain natural reproduction well-recognized methods of silvicultural practice must be adhered to (Troup, 1928: Hawley, 1946).

5. Methods of Natural Reproduction from Seed. — The methods of natural reproduction under all silvicultural systems fall into two main classes:

1. Natural reproduction from trees standing over the area to be regenerated.
2. Natural reproduction from trees on the border or at one side of the area to be regenerated.

When the trees standing over the area to be regenerated are of all ages, and as they mature are removed a few at a time, the method of regeneration is called selection. When the trees are relatively even-aged and the timber is removed in two or more fellings at relatively short intervals during the process of reproduction, the method of regeneration is called shelterwood. In the selection method regeneration is continuous and the resulting stand is all-aged. In the shelterwood method the period of regeneration extends over a limited part of the rotation, usually from 10 to 15 years, or the time between the first and the last fellings, in the removal of the crop; the resulting stand is relatively even-aged. The selection and shelterwood methods often are combined in practice and the period of regeneration extended to 30, or even 50 years, as is the present practice in parts of the Black Forest in Germany.

6. Selection Method. — Natural reproduction is most easily attained in forests managed by the selection method, although in such forests it is often difficult to regulate composition. The selection method is applicable to stands represented by trees of all ages. In such stands, trees are taken out here and there as they mature and the younger trees remain standing. Only a small percentage of the entire stand is cut at one time. The openings made by the removal of single trees or small groups of trees are always small. They are often made at the margin of existing openings already filled with reproduction. Because of the abundance of seed trees and the protection afforded the soil, openings are quickly filled with young, vigorous trees. Reproduction in a selection forest most nearly approaches that of a virgin forest, the chief difference being that in the selection forest small openings are made by the removal of mature trees, but in a virgin forest openings are made through the death and decay of the overmature trees. When there is an abundance of reproduction, tolerant species will often crowd out or suppress the less tolerant ones.

7. Shelterwood Method. — The shelterwood method is applicable to relatively even-aged stands. The mature crop is removed gradually by a series of cuttings. Ten to fifteen years usually intervene between

the first cutting and the removal of the last of the crop. During this interval reproduction takes place. From the standpoint of reproduction, this system has many advantages. The cuttings leave a large number of seed trees more or less uniformly distributed. The shelter of the overstory protects the soil and the young seedlings and retards the growth of weeds, grass, and shrubs. Seed is provided in abundance and is well distributed. As new growth is established before the last of the overstory is removed, the soil is not exposed as it is in clear cutting.

8. SEED-TREE METHOD. — The seed-tree method was used largely throughout Europe during the 15th and 16th centuries to supplement artificial regeneration and natural seeding from adjacent stands. It has been used in the United States in recent years but will result mainly in disappointment.[1] Except with the most resistant species, the seed trees left are liable to be windthrown. The species must produce seed susceptible of wide dissemination by the wind, the soil must be receptive, and reproduction must be obtained quickly or a growth of herbaceous and other vegetation will prohibit later regeneration.

9. CLEAR-CUTTING METHODS. — After the removal of the mature timber in one cut, regeneration after cutting is obtained by seeding in from the marginal stand or from trees cut in the clearing operation. When seed trees are wholly or for the most part in adjacent stands, the seed must be light, capable of being widely disseminated by wind, and distributed over the area for a considerable number of years. All methods of reproduction from seed trees not standing over the area to be regenerated are much more uncertain than either the selection or shelterwood methods. When the area is clear-cut or denuded by fire or other causes, soil deterioration is likely to occur and the ground become covered with a more or less dense growth of herbage, making regeneration more and more difficult the longer it is delayed. Clear-cutting methods are all more or less unreliable, and, when they are used, it may sometimes be necessary to supplement them by artificial regeneration. A notable exception arises when there is a sufficient amount of viable seed on the ground at the time of the clear cutting to restock the area adequately. This is illustrated in clear cutting of maritime pine in France and loblolly pine in the southern United States after good seed years.

When regeneration is wholly or in part from seed trees standing on

[1] Except with the southern pines and possibly on moist sites in the Southern Appalachian region where regeneration of light-seeded, relatively light demanding species is desired.

areas adjacent to the tract where reproduction is to be established, the methods are:

1. Clear-cutting in strips.
2. Clear-cutting in patches.

10. *Clear-cutting in Strips.* In general, the effectiveness of the strip method depends upon the width of the strips; the narrower the strips, the more abundant and uniform the distribution of the seed and, under favorable soil conditions, the better the reproduction. For most species the strips will range in width from 1 to 4 times the height of the stand. The success of this method depends also upon the point of beginning of cutting, the direction of the strips with reference to the prevailing wind, and the shade cast by the remaining stand. The strips may be cut alternately or arranged in progressive series.

11. *Clear-cutting in Patches.* When the area to be regenerated is clear-cut in patches, the openings should be small, about an acre or less in area. The smaller they are, the closer the approach to the selection and the shelterwood methods. In the practice of this method, advantage is usually taken of openings already existing in the stand due to wind or other causes, and their area is gradually increased with the progress of reproduction. This method of reproduction has been used successfully with even-aged loblolly pine in the Duke Forest in central North Carolina.

12. Successful Natural Reproduction from Seed. — Successful reproduction means the establishment of trees of desirable species in numbers great enough to yield a satisfactory stand. Without close observation, reproduction is likely to be misjudged because most species reproduce unevenly. In some places it will be too dense and in other places it will be entirely absent. It is not the number of trees per acre that constitutes good reproduction but how well they are distributed. Nature frequently sows more abundantly than is necessary or even desirable. An overly dense stand is usually unable to develop satisfactorily. Growth in height, diameter, and volume is retarded. Douglas fir, red spruce, lodgepole pine, jack pine, white pine, and many other species both of conifers and hardwoods often reproduce in stands too dense for satisfactory development. How close the seedlings should stand during the first few years in order for the reproduction to be complete depends upon the species, site, and methods of management. Species that naturally develop straight boles and narrow crowns of small branches can safely stand much farther apart than species which must be crowded from the side in order to

attain good form. Thus white pine and red spruce need be no closer than the average planting distance for the species, namely, 4 to 6 feet. On the other hand, oak and beech can scarcely be too close. A natural reproduction which produces from 15,000 to 25,000 seedlings per acre is not too dense.

13. Continuous and Discontinuous Reproduction. — In a natural forest, in its climax form, reproduction is continuous year after year but, when the natural forest is disturbed by man or other external agents, reproduction becomes more or less discontinuous, very abundant at certain times and little or none at other times. All silvicultural methods of treating stands in order to attain natural regeneration, except the selection method, aim to attain complete regeneration in as short a time as possible. This period, however, may extend over a space of from 1 to 50 years, depending on the silvicultural practice and the species and local conditions of climate and soil. It is seldom that a complete stand can be attained from a single seed year. Whatever the time is, it is termed the period of reproduction.

14. Problems of Natural Reproduction. — There are two quite distinct sets of problems involved in natural reproduction of stands:

1. Reproduction in clearings.
2. Reproduction within stands.

The first relates to the production of an entirely new stand after the removal of the first. The second relates to the filling up of blanks in an old stand by new reproduction or the establishment of advance reproduction under shelter, which later can be used as a basis for a new crop.

15. Reproduction in Clearings. — The completeness of reproduction and time required for reproduction from seed in clearings depend primarily upon the size of clearing, viability of seed on the ground when the clearing is made, and the dissemination of seed from trees on its border. The term "small clearings" may be applied to areas that are capable of becoming fully stocked from a single generation of seed trees on the border. Large clearings are those so extensive that more than a single generation of seed trees is required for fully stocking the area. The character of reproduction depends not only on the size of clearing but also on condition of the soil and ground cover, the climate, and particularly direction of the prevailing winds during seedage for all wind-disseminated species. Although it is not possible to predict the year that reproduction will take place under given conditions, it is often possible to determine in a broad way the period within

which reproduction will take place in a given case and what will be its character.

Not infrequently after denudation, the ground is immediately covered with a more or less dense growth of herbaceous plants and with low shrubs or seedlings other than those desired; and a long period intervenes before the desired species reestablish themselves. The period of reproduction is approximately the difference in age between the oldest and youngest trees in the new stand. One or more years must be added to span the period from denudation to the time the first seedlings become established.

A study of natural reproduction involves the study of forest succession. A study of reproduction is not merely an enumeration of species and their listing as to frequency and abundance. It involves a forest in all its stages of development from seed production to decadence. Foresters dealing with reproduction after denudation must be able to account for satisfactory reproduction in certain places and at certain times and unsatisfactory reproduction in other places and at other times. They should know the relation of grazing, fires, and other agencies to bare areas and the possible extension of forests beyond their present limits.

In studying natural reproduction on small clearings a forester determines how many seed trees should be left on the border of the openings in order to obtain the distribution of seed over areas of different size, form, and topography; also how large a clearing can be made under different circumstances and still maintain soil conditions suitable for the germination and establishment of the seedlings.

There are many conditions where the first growth following a clearing is different from that previously occupying the ground. A case in point is in eastern Massachusetts, where pure white pine is frequently followed by a stand of mixed hardwoods. Again, pure spruce is often succeeded by birch or maple, or both in mixture. In New England, clearings by fire are frequently succeeded by birch, aspen, and cherry. If there are seed trees on the border of the clearing, the original species will return after a time, when because of their slower growth they form an understory and at first make but little imprint on the stand. Later, however, they grow up through the birch and other light-foliaged, intolerant species, overtop, and destroy them.

The problem of reproduction on large clearings, such as extensive areas denuded by fire, of common occurrence in the Lake States and in the West and South, must settle the question of artificial regeneration or the reestablishment of forest conditions on such areas by natural

reproduction. Under ordinary circumstances very large clearings can not be restocked from the seed trees now standing on the border. It is usually a question of the slow migration of the forest on the clearing by successive generations of trees. The seed trees now standing distribute seed as far as the wind will carry it, and reproduction occurs in greater or less amount within that range. Near the seed trees the stand may be good, farther away it is more open, and still farther there are merely scattered trees representing the seed borne to unusual distances by exceptional winds. As soon as the trees of the first generation are large enough to bear seed, reproduction occurs in the openings about them and there is a further advance of the forest. This continues until the entire area has been restocked. Since it takes 20 to 50 years for the trees to bear seed, the rate of advance of the forest is slow. Centuries will be required to restock by this method some of the large devasted areas in the West and South and in the Lake States.

16. Reproduction within Stands. — Many silvicultural problems center in reproduction within stands. Natural reproduction, following partial cuttings or very heavy thinnings caused by various agencies which remove only a portion of the trees of a stand, is important. It also involves reproduction following ordinary methods of forest exploitation which almost invariably leave a varying number of culls and unmerchantable trees on the ground. In scattered seed trees and reproduction on land not entirely denuded the problem is primarily concerned with the period of reproduction and the composition of the resulting stand. It is also concerned with the condition of the seed trees, their number and distribution over the area, and how they should be selected in order to obtain complete reproduction. In stands exploited for one or more of the more valuable species the important silvicultural problem is the reproduction of the valuable species and the elimination of the undesirable trees. In the shelterwood method of regeneration, to facilitate reproduction a preparatory opening of the stand increases seed production and improves soil conditions for the reception of the seed and for germination. A further opening of the stand later on stimulates growth in the young plants and makes establishment possible. Germination studies determine when and how the cuttings must be made, how much of the stand must be removed in each cutting, and in mixed stands what species will appear in the reproduction and the relative amounts of each. In order to make a successful reproduction cutting under the shelterwood method, one must know to what extent and how the trees should be isolated in each stage of the process so that reproduction may be established.

A forester, therefore, must determine the correct location, character, and number of seed trees which should be left to obtain the distribution of seed over openings of different sizes, and he must know how large an opening should be made under different circumstances in order to obtain germination of seed and establishment of the seedlings. If the trees have winged seeds the question of their distribution is comparatively simple. If the soil is dry, or the site exposed to drying winds, there may be a problem of protection of the soil and seedlings from drought, and the size of the opening may be the determining factor. In a mixed forest the favoring of one or more of the most desirable species may be attained by varying the size of the opening. If the site is in danger of being overrun by weeds and shrubs, or in other ways deteriorating, the severity of the cutting may be reduced and reproduction still be obtained. A forester has these practical points in view when he studies reproduction. His first endeavor is to determine the facts by studying openings of different sizes which have been made in the past. He finds a variation in the reproduction of the different species, a retarding of reproduction, or entire failure, under different circumstances. He makes observations on a large number of different cases, describing with care the present conditions of the stand, its probable condition before cutting, the size of the opening, the character of the soil, and other factors which may have a bearing on the reproduction. From records of reproduction in carefully selected places one is able to determine what happens in different stands which have been opened up in different ways.

17. Study of Natural Reproduction. — As a knowledge of natural reproduction is the key to the successful development of forests and to methods of silvicultural management and protection, the methods for the study of reproduction are worthy of detailed and special consideration. The mere recording of the frequency and abundance of reproduction is of little silvicultural value, but the reasons for its presence or absence are of the highest value. In order to explain these scientifically it is necessary to initiate and conduct various lines of research over more or less extended periods of time.

Since the study of natural reproduction is not merely a study of the actual seedlings that chance to be on the ground at a given time but involves a forest in all its stages of development, from the production of seed through the development of the stand to its decadence, the time element must be considered. A thorough study of plant succession is essential in every serious research on natural reproduction. Thus the accounting for bare areas after burns and excessive grazing involve

studies of natural reproduction. The explanation of the kind of natural reproduction following partial denudation by lumbering, insects, and disease must be ascertained. So also the absence of forests in certain localities now covered with herbaceous and shrubby vegetation may have to be explained through studies of natural reproduction.

In the study of reproduction a forester must consider and in some instances measure the site factors which account for plant succession. He must gain a historical knowledge of the particular site he is studying from the standpoint of the causes of succession in its various stages. He must consider the varied effects of climate and soil upon each of these stages and also the effects of various biotic factors. Furthermore, in this study, all parts should have a direct or indirect bearing upon practical results and be useful in attaining better reproduction in forestry practice.

Biotic agents must not be overlooked in studying natural reproduction and determining the causes of success on some sites and failure on others. Thus poor seed may be due to inferior seed trees or to disease or insect depredations while the fruit is developing. It may be due to seed-destroying fungi or insects. Through their denuding influence, fire, lumbering, and grazing may materially affect natural reproduction.

18. Effect of Fire on Natural Reproduction. — Fires may be caused in many ways.[1] The accidental starting of forest fires depends upon the season and condition of the weather. Although all fires are equal when they start, they differ in their behavior later, depending upon the particular conditions under which they start. They may develop into surface fires, ground fires, or crown fires.

Surface fires consume only the surface materials such as dried leaves, twigs, and other parts of the litter. They do little direct damage to mature timber when the bark on the trees is thick enough to resist them. They are a very serious menace to reproduction, for young trees of all ages up to the time that the bark becomes sufficiently thick to resist the fires are likely to be killed. Trees may become resistant after 10, 20, or more years, depending upon the species and the severity of the fire. Surface fires even in young stands seldom cause complete denudation. In most hardwoods, the roots of young trees quickly sprout and reestablish the stand. Unless the seeds lie in moist litter below the inflammable material and thus escape injury they are destroyed by surface fires.

[1] The important literature dealing with the causes and effects of forest fires has been summarized by Hawley (1937).

Although not common, ground fires are a much greater menace to natural reproduction than surface fires, for they destroy all the dead organic matter sufficiently dry to burn down to the mineral soil. They occur during very dry periods in regions having large accumulations of litter and peat. They usually destroy all the vegetation including trees of all ages; furthermore, seed stored in the ground above the water table is destroyed. Seeds of some species, notably southern white cedar, below the water table at time of a fire may escape destruction, germinate, and reestablish the stand (Korstian, 1924). Since the roots of the trees are destroyed, they have lost their capacity for sprouting or reproducing from suckers. A single ground fire may cause complete denudation, which necessitates migration for the establishment of a new stand.

Crown fires are usually the most severe and most extensive of all fires. When a crown fire occurs where the forest floor is moist or wet, although all the vegetation above the forest floor is killed, nearly all the litter is left unburned; consequently the germinability of the seed in the litter and soil is unimpaired. When the litter and humus are dry and consequently destroyed, migration is necessary for the establishment of a new stand.

In studying the effect of fire on reproduction, special attention should be given to its effect on the forest floor, as the intensity of the fire and its far-reaching effect on reproduction may be indicated by the degree to which the litter and humus have been destroyed, and, as a consequence, the destruction of seed and sprouting capacity.

19. Effect of Lumbering on Natural Reproduction. — Logging operations conducted without particular reference to natural regeneration seldom remove the entire stand. However, following this type of lumbering the cut-over areas are rarely left in the best condition for optimum natural regeneration. Such trees as may be left are generally small, poorly formed, unmerchantable trees of little value for seed production, often of undesirable species.

Cutting operations conducted in accordance with silvicultural methods aim toward attaining reproduction by clear cutting, selection cutting, isolated seed trees, grouped seed trees, shelterwood, or coppice. The manner of harvesting the mature stand determines not only the possibility of natural reproduction but also the species in the reproduction. When clear cutting is practiced, the reproduction that follows is determined not only by the width of the cleared strip, the bordering seed trees, and the distribution of the seed but also by the soil conditions for germination and establishment and the amount of

viable seed in the litter and soil. When isolated seed trees are left, the reproduction that follows depends upon their capability for the production of seed, their resistance to wind throw, their frequency, and the condition of the soil during the entire period of reproduction. The grouping of seed trees reduces loss from wind throw but is less advantageous for seed distribution. Selection and shelterwood methods of cutting are most favorable for ample reproduction as they stimulate seed production and its equal distribution and at the same time render the soil most favorable for germination and establishment, owing to the protecting overstory.

When a stand is felled, with the expectation of obtaining coppice or sprout reproduction, special attention must be given to the age of the stand and the time of cutting, as well as the effect of fire and grazing upon sprouting capacity. Sprouts usually develop more rapidly than seedlings, mature earlier, and produce trees of smaller size.

20. Effect of Grazing on Natural Reproduction. — Grazing affects natural reproduction advantageously in facilitating seed distribution and in covering the seed by trampling. It is sometimes advantageous through selective browsing. The stock, by grazing on the competing vegetation, to a greater extent than on the crop trees, reduces competition. It affects natural reproduction disadvantageously by destroying the seed and young plants of desirable species. By rendering the soil more compact it makes germination and establishment more difficult. Therefore, grazing may disastrously affect natural reproduction both directly and indirectly; directly insofar as it affects the reproduction itself and indirectly through its effect on the soil.

The unrestricted grazing of hogs in the forests of longleaf pine effectively prevents reproduction, as the hogs consume a large part of the seed before germination takes place and search out and consume the young seedlings after germination takes place and before they can grow beyond the period of damage. By consuming the mast, hogs are destructive to the reproduction of oak, beech, and many other broad-leaved species.

Sheep and goats are chiefly harmful to natural reproduction in that they feed upon most species of hardwood and, when other food is limited in quantity, upon most species of young conifers. The amount of damage is closely correlated with the extent of the grazing. More or less damage is done by trampling, thus making the soil less favorable for germination. Ordinarily less damage is done by cattle and horses than by other domestic animals.

21. GROWTH OF STANDS

Growth is of fundamental importance in forestry since it determines the increment and yield of stands. The growth of stands progresses differently from the growth of individual trees; neither height and diameter nor basal area develops in the same way. Volume increment is controlled by a large number of variable factors. The amount of wood that a well-stocked stand of a given species lays on in a single year depends on its age, freedom from external disturbances, quality of site, and favorableness of the growing season. It also varies with the species but is not at all proportional to the number of trees per unit of area, provided the canopy is unbroken. Thus a plantation of white pine spaced 10 by 10 feet is likely to yield as much wood at the end of the rotation as one spaced 4 by 4 feet, provided the site quality is the same. The quality, however, will not be the same.

22. Increment in Stands

As the increase in the volume of a stand is variable one year with another and does not continue indefinitely, current increment, periodic increment, and mean increment are employed in studying growth. Current increment is the growth of a single year; periodic increment, of a definite period in the life of the stand, usually 10 years; and mean increment is the average annual growth over the period of the rotation or up to a given time in the life of the stand. Increment is seldom studied for a single year. A 10-year period is none too long to eliminate variations in growth due to fluctuations in climatic conditions and other causes. The volume increase compared with the total volume of the stand is the growth percentage. Periodic annual growth is commonly used as the basis for computing growth percentage. In an even-aged stand current annual growth in volume increases very slowly when the stand is young; it increases with more rapidity until the maximum is attained near middle age, after which it falls off with the beginning of decadence of the stand. If a graph is made in which the current annual increment and the mean annual increment are plotted on age as the independent variable, they will cross when the current growth for a given year equals the mean for the entire period of growth. Prior to this time the current annual increment exceeds the mean, but later the mean exceeds the current. The point where the curves cross marks the culmination of the highest mean annual increment.

During the first few years in the life of a white pine stand spaced 6 by 6 feet, the current annual increment may not exceed 0.5 to 5 cubic

feet per acre. It attains its maximum when the stand is 40 to 60 years of age. Although the maximum annual increment is attained at a comparatively early age in the life of the stand, the mean annual increment continues to rise for a number of years and reaches the maximum when the current and the mean are equal. The year of maximum mean annual increment terminates the period at which, if harvested, the stand will produce the greatest yield measured in average years. It does not as a rule mark the economic maturity of the stand. After the mean reaches its maximum it may continue at about the same level for a number of years. The rate of diminution depends largely on climatic and soil conditions. Under favorable conditions the decrease is rapid. The basal area gradually increases throughout the entire economic life of the stand.

Too heavy thinning of the stand may cause too large openings in the crown cover. When large openings are made, intolerant species find suitable conditions for satisfactory reproduction. For this reason, when stands are opened sufficiently for the reproduction of intolerant species, there is a marked falling off in current annual increment. In a few years, however, if the crowns again close, the increment returns to its former condition. When small openings are made in the crown cover, as when the crowns are separated from each other, yet not so wide as to leave space between for other trees to develop, the condition is the best for the growth of intolerant species. This is often the natural condition with such species. On the other hand with tolerant species it is not natural and is brought about only by artificial interference which greatly reduces the number of stems per unit of area.

23. Effect of Thinning on Growth

When a dense stand is opened by thinning, the remaining trees grow faster than previously. The increase of growth in diameter is often 100 percent, and, not infrequently, a stump shows annual rings 3 or 4 times as wide as before the thinning. If a tree has a fairly well-developed crown and is growing in a closed stand, the opening of the stand admits more light to the lower part of the crown and reduces root competition for soil moisture and nutrients. The result is a distinct increase in growth sometimes beginning the first season after thinning. There is not only a stimulated diameter growth through this increased intensity of assimilation, but the crown as well increases in size. At the same time, the root system is enlarged proportionately and there is a sustained growth greater than before the new conditions

were established. This increase in growth takes place only when the tree is capable of responding to the new forces which stimulate its activities. The conditions under which no increase takes place are:

1. When a tree is dominant, its crown is not crowded from the side, and it has ample root space. This condition exists when trees are growing in open stands in need of little or no thinning.

2. When a tree has been crowded or overtopped so long that it is not vigorous enough to respond to the new conditions. Sometimes overtopped trees gradually respond to increased crown and root space, and in 3 to 5 years after a thinning assume a more rapid growth rate. The question of whether a crowded or overtopped tree is capable of recovery is one of the most important problems with which a forester has to deal in making thinnings. The answer can sometimes be found in the proportion of the crown length to the total height of the tree.

3. When the soil is too poor to supply the necessary nutrients and water to meet the new activities of the tree. A thinning on a dry soil may not result in increased growth of the stand, but there may be a retarded growth because the removal of part of the forest cover causes the soil conditions to become less favorable.

The increased growth in a tree after a thinning has been made is not uniform in different parts of the bole. It is greatest at the stump. Sometimes, the increase at the stump may be several times greater than elsewhere. There may be a marked increase at the stump and none elsewhere; or there may be an increase at the stump and at the base of the crown but none at all half way up the bole.

Hartig (1891) states that the sudden increase in growth on upland soils is largely due to the release of a large amount of available nutrients through rapid decomposition of litter. It is chiefly due, however, to increased root space on upland soils and the consequent increase in available moisture. The distribution of the increase is the result of mechanical stresses caused by the wind. The strain is increased at the stump after a thinning and hence there is the greatest need for large dimensions there. It is greater near the crown than in the middle of the shaft for the same reason.

24. YIELD OF STANDS

The amount or volume of timber in a stand per unit of area at a given time is usually known as *growing stock*. *Yield*, on the other hand, is the volume produced by a stand of a given composition at a given age or over a definite period of time under given site conditions and treatment. The total volume of a stand at any given time is the

yield of that stand for its entire period of growth to the given age, provided no part of the stand was removed earlier in thinnings. The primary purpose of studying yield in existing stands is to enable the prediction of future yields in young stands now growing and even in stands yet to be established.

Future growth in volume is predicted either by projecting the rate of growth in existing stands into the future or by accepting past growth in existing stands as an indicator of future growth on similar sites under similar conditions. The former method aims to project the growth in a given stand for a period of 5 to 10 years, hence from the actual measured growth of the past 5 or 10 years. It is assumed that the rate of the immediate past will remain unchanged in the immediate future or, if found to have changed, that the same rate of change will continue; and this can be predicted by the projection of past growth curves into the future. The latter method has for its purpose the prediction of the probable yield from various qualities of forest land. This method assumes that the yield of stands, whose past growth has been measured, indicates future yield; that a relation exists between stands whose yield is known and stands whose future yield is sought.

The measurement of yield in existing stands on different qualities of site, at regular intervals over the life of the stands, or the measurement at one time of stands of various ages, usually in 5- or 10-year age classes and growing on different qualities of site, provides the data for the construction of tables from which yield can be predicted.

In the application of these tables, however, the predicted yield for a given stand can not be expected to coincide exactly with that shown in the yield tables even when separate tables are available for each site class, because no two sites are exactly the same in site quality and in forest cover. Yield tables derived from periodic measurements in the same stands are considered more acceptable than similar tables derived from measurements at one time in stands of different ages. In the former tables the past history of the stands is known and the measurements are repeated on the same sites. In the latter the past history is unknown and the measurements are taken on different sites.

25. Factors Affecting Yield of Stands

The increment or total volume production on a given area is controlled by the following factors:

1. Species.
2. Composition.

3. Site quality.
4. Form.
5. Density.
6. External disturbances.
7. Silvicultural treatment.

Some species like yellow poplar, aspen, and some of the pines grow much more rapidly than others, as oak, hickory, beech, and hemlock. Even on the same site quality and under similar conditions of stocking and freedom from external disturbances, a given area will yield more of one species than of another.

The composition of the stand is a factor in its yield. A pure stand on the whole has a lower increment than a mixed stand only when the mixture is composed of compatible species. Thus a pure stand of Scotch pine in Germany has a lower yield than a stand composed of 90 percent pine and 10 percent beech. So also a pure stand of oak yields less than a stand of oak and beech. In general the increment of a mixed stand is greater because of a more complete occupation of the site. The amount of increase depends on the extent to which the species in the mixture make unlike demands on the site.

Site quality refers to all the climatic, edaphic, physiographic, and biotic factors of the environment which influence growth. Because of differences in site, the yield from one site quality may be greater than from another. Both the yearly rate of growth and the total growth over a period of time depend directly or indirectly on the site factors, which determine site quality.

The form of a stand refers to the age classes comprising it. An even-aged stand growing on a site similar to that bearing an uneven-aged stand is essentially different in character and the yield is not the same. The maximum number of trees are in the upper crown class in the even-aged stand. In uneven-aged stands, on the other hand, each tree is in competition, not only with trees of its own age but with those older and younger as well. The older age classes occupy more space than the younger and on the whole encounter less competition than the dominant individuals in an even-aged stand, and the rate of growth after a tree becomes dominant is more rapid. They may, however, have experienced a more or less extended period of oppression before becoming dominant, as is often the case in natural stands. The younger age classes occupy a relatively small percentage of the total space although the individuals comprising them far exceed in numbers those in the older age classes. The annual growth in the uneven-aged stand represents the growth of all the age classes present on the area.

In general, any degree of stocking which provides a continuous canopy gives the maximum growth. All natural stands tend to approach normal density of stocking through crown expansion. Natural spacing, however, becomes largely a matter of chance and often fails to attain full stocking. Although the tendency is to approach normality through crown expansion, there are places in which the canopy is incomplete and growth reduced. A greater yield from artificial stands uniformly spaced is largely dependent on the degree to which they are able to maintain a full canopy continuously during the rotation — the predetermined age at which the stands are to be cut and reproduced.

The degree to which a stand is beset by natural enemies, as insects and fungi, influences increment, for it affects the completeness of stocking. So also adverse weather conditions, climatic factors, such as wind storms and ice storms, open holes in the canopy which reduce volume production of the stand. Stands develop either under natural conditions, as in a virgin forest, or under silvicultural treatment. Since the yield of merchantable products per unit of area, such as lumber and dimension materials, and the value of these products depend more upon the species, number, size, and form of the trees brought to maturity in the stand than upon the total volume, silvicultural treatment aims to maintain the most suitable crown density throughout the life of the stand and at the same time to give the maximum number of trees sufficient growing space to enable them to attain their best size and form. Although it is generally recognized that a fully stocked stand is one that has an unbroken canopy without regard to the number of trees, stands that are fully stocked when young soon become overstocked. Unless the stand exhibits great variation in dominance, overstocking results in dwarfing all trees alike and a falling off in growth. These natural tendencies to overstocking and the consequent falling off in growth are markedly influenced by artificial control. Silvicultural treatment stimulates growth in the crop trees by removing the others that compete with them for growing space. Initial spacing and subsequent thinnings determine the number of trees per unit of area at each period in the life of the stand. This should be the optimum number that the site will support with due regard to form, height and diameter growth, and quality increment. Ideal conditions for the highest yield in stands result from maintaining normal stocking and the preventing of overstocking by repeated thinnings which maintain a proper balance between them and the remaining stand. As this treatment stimulates growth in the crop trees the rotation for the growing of products of definite sizes can be shortened.

It is the aim of a forester to obtain just that density which will produce the highest yield and, at the same time, grow trees of the dimensions and quality of wood, which will best meet the requirements of the market.

CHAPTER XVI

TOLERANCE

1. CONCEPT OF TOLERANCE

Tolerance is a term commonly used to express the capacity of a tree to develop and grow in the shade of other trees. The tolerance of a species gives an innate character to its growth and development and to forest types in which it is prominent. Thus differences in the relative tolerance of various species may cause radical differences in both the physiognomy and stratification of a forest. A tolerant tree grows well in the shade of other trees and an intolerant one does not. Nearly every tree in a forest must develop in competition with other trees in the stand. Therefore, the concept of tolerance has undergone some modification during the last quarter of a century in recognition of the fact that tolerance involves more than merely shade tolerance. Other site factors in addition to light affect the growth and development of trees under forest canopies.

Where trees are grown under the shade of artificial canopies, such as cloth of different weaves, the intensity of light reaching them causes certain definite reactions in the trees. When the same trees are grown under natural canopies, where the intensity and quality of light are similar to that under the artificial canopy, the reactions may be entirely different. Under the latter condition, trees forming the natural canopy not only affect the light that reaches the subordinate vegetation, but through root competition for growing space they profoundly affect other factors such as available soil moisture and nutrients. Such factors may become significant before the light is reduced by the canopy to the point where photosynthetic activity is less than the outgo of energy by respiration. The disappearance of seedlings before light intensity becomes the most significant factor is often due to root competition for soil moisture and soil nutrients, or to some other factor becoming critical. Thus in ordinary upland forests the absence of reproduction and other subordinate vegetation may be due either to the light intensity's being reduced to the point where it becomes most significant or to some other factors, such as available soil moisture. It is only on sites where the available soil moisture or factors other than light are not critical that the canopy becomes sufficiently dense to make

light the most significant factor. In the forests of the Olympic Peninsula in the northwestern United States, where there are 100 or more inches of annual precipitation and where available soil moisture is not a critical factor, a canopy which excludes 85 to 95 percent of full sunlight does not inhibit the development of a luxuriant subordinate vegetation. Farther east, where the annual precipitation is 30 inches or less, a relatively open canopy which excludes less than 60 percent of full sunlight may inhibit the development of subordinate vegetation. Available soil moisture, through root competition, has become most significant.

The first real challenge to the concept that tolerance was primarily concerned with light conditions in forests came when Fricke (1904) studied the effect of the elimination of root competition by trenching around small, poorly developed Scotch pine reproduction under a forest canopy of the same species. He found that the presence, growth, and development of tree reproduction, shrubs, grasses, and mosses on the forest floor depend very little upon light intensity but mainly upon the degree of soil desiccation caused by competition of the roots of the older, overstory trees.

If tolerance is accepted solely as a light relation, Burns (1916) has pointed out that it can not be measured by the relative vigor shown in reproduction and in the growth and development of subordinate vegetation under different densities of overstory, because relative vigor is determined by all the physical and biotic factors of the site and not by light alone. Although there is no other physical factor so strikingly altered by variations in the density of the canopy as is light, other factors are altered and can not be ignored. Poorly developed and weak tree seedlings and herbaceous vegetation on the forest floor are associated with weakened and reflected light which reaches them through the canopy. The senior author has demonstrated that the almost complete arrest of growth in white pine under a dense stand of gray birch is not due to light shortage. Adams (1935) found that thinning in a 20-year-old white pine plantation which reduced the basal area by 45 percent resulted in significant changes in several other site factors besides light. Thinning was followed by increases in basal area per acre and in height growth, diameter growth, and volume increment of selected final crop trees. As was to be expected, an increase was noted in total solar radiation reaching the forest floor. There were insignificant increases in air temperature, soil temperature, evaporation, and in amount of rainfall passing through the crown canopy. Thinning in an 18-year-old Scotch pine plantation which re-

duced the basal area by 30 percent gave much the same results except that a significant increase in evaporation was recorded for the thinned area. Thinnings in stands of both species resulted in a statistically significant increase in the percentage of available soil moisture when the water content of the soil was low.

Dense stands of white pine and other species in New England without subordinate undergrowth may be invaded by an abundant vegetation in quadrats isolated by trenching which eliminates root competition (Toumey and Kienholz, 1931). Available soil moisture in trenched quadrats during critical periods in the growing season may be 2 to 9 times as great as in untrenched check quadrats. It is evident from trenching experiments that the absence of certain species under canopies and the poor growth of those that persist are due in part to the effect of trees forming the canopy on soil moisture and other soil factors and that light intensity and quality are apparently not always the limiting factors.

Aaltonen's (1926) studies in Finland are in accord with the above results. He concludes that there exists between the members of each species a very definite space arrangement which is directly dependent upon quality of the soil. He states that under natural canopies height of the seedlings and their distance from the mother tree are in definite relation to each. On a poor site few seedlings appear, even in an open stand, in close proximity to the boles of the mother trees, and those that appear are poor and stunted. This is often the case in a shelterwood cutting on poor, dry soil. If, however, the site quality is superior, an abundance of seedlings appear, after a shelterwood cutting, not only in the small openings but also directly beneath the canopies of the remaining trees. Here soil moisture is not critical. In general, a definite space arrangement exists within a stand for each site and soil type of different productivity. The poorer the site (soil quality), the larger the growing space (root space) necessary for each tree. Aaltonen states that it is obvious that this is not entirely a light relation. The space arrangement of those parts of the trees above the soil is determined mainly by their roots and the competition existing between them for moisture and soil nutrients.

The importance of factors other than light in determining the establishment and growth of vegetation under natural canopies has been stressed by the work of Fabricius (1927, 1929), Toumey and Kienholz (1931), and Korstian and Coile (1938), besides that of Fricke (1904) already mentioned. Fabricius (1927, 1929), in studying characteristic reactions of tolerant and intolerant species to the light and soil moisture

conditions of forests, concluded that tolerant species are naturally better adapted to withstand the drought conditions of a forest because their more efficient CO_2 assimilation under low light intensities enables them to develop extensive root systems more rapidly than intolerant species under similar conditions. Thus he regards shade, as well as root competition, as important in influencing the growth and development of the young understory, although soil moisture, relatively considered, may still be the controlling factor.

As time elapses and root competition within trenched plots increases, other significant changes occur. Toumey and Kienholz (1931) report that by the sixth year after trenching height growth of white pine was declining on their plots. Fifteen years later or 21 years after the plots were established Lutz (1945) rechecked one of the trenched plots and found that all the white pines were dead and that the hemlock had flourished, having increased in both numbers and size. He concluded that radiation intensity was too low for the white pine but was favorable for the shade-tolerant hemlock.

The trenched plots in the Duke Forest, although not trenched for as long a time, are already beginning to show similar effects. The loblolly pines are becoming spindly and unthrifty; some have died, and the death of others appears certain. Understory hardwoods are increasing as is typical in Piedmont pine stands. Apparently sufficient water is available for growth of the hardwoods. Furthermore, the hardwoods have the capacity to sprout after dying back as a result of drought, while pine seedlings growing on the forest floor die outright during periods of drought. Loblolly pine seedlings grown in open fields have much deeper and better branched root systems than those grown under forests stands (Coile, 1940). Kramer and Decker (1944) found that hardwoods are photosynthetically more efficient than pines at low light intensities, and they suggest that the lesser growth and smaller root systems of pine seedlings grown in the shade are likely to be the result of inadequate photosynthesis. Although the pines can survive under moisture conditions equal or inferior to the needs of the hardwoods when the intensity of solar radiation is ample for photosynthesis, it appears that in the shade the pines are unable to carry on the physiological processes resulting in successful growth. Oosting and Kramer (1946) clearly emphasize the interrelationship of the complex factors involved in competition by stating that " survival and growth of pines require a light intensity which is high enough for them to produce enough food to develop root systems capable of absorbing the necessary water." In other words not only the environmental factors of solar

radiation, soil moisture, and dissolved nutrients but also the relative photosynthetic efficiency and root habit and development are involved in tolerance.

Under the very different conditions of the Southwest, Pearson (1923) found that tree shade favors germination and early survival of ponderosa pine seedlings by checking excessive evaporation and high temperature at the soil surface, but that later survival is poor. Many of the seedlings which are shaded by trees during a considerable portion of the day encounter competition for soil moisture from the roots of older trees and thus may fare worse from the standpoint of moisture than seedlings exposed to full sunlight but beyond the influence of tree roots. The undernourished appearance of the ponderosa pine seedlings is usually considered to be due to deficient light, but Pearson (1923) regards heat to be as important as light for photosynthesis, or more so. Krauch[1] reports that Douglas fir seedlings, to survive in the Southwest, definitely require some shade during their early stages of development. This would seem largely to explain why good stands of fir seedlings occur under or near small groups of trees that cast relatively light shade, such as the pines, oaks, and aspens, and why very few seedlings are found directly in the open.

After reviewing the reaction of jack pine, Norway pine, white pine, and white spruce seedlings to nutrient deficiency, to drought, and to heat, as well as their rate of growth after release from suppression, their rate of root penetration, and their first-year survival on the forest floor, Shirley (1943, 1945) concludes that the survival of these species under forest canopies in the Lake States and their position in the successional series toward the climax forest type are dependent primarily upon their "shade tolerance." In an effort to simplify the concept of tolerance he urges that the term "tolerance" be used only with reference to a specific site factor and that tolerance of low light intensity, deficient moisture, deficient nitrogen, or heat or cold be called shade, drought, low nitrogen, heat, or cold tolerance. However, he (1945) states that "either shade or root competition may be limiting factors in the growth of young conifers." Although considerable progress has been made in the clarification of the basic concept of tolerance, the practical application of this suggestion will not be possible until further research has more clearly brought out the role that each factor plays in competition. The same factors usually are not limiting on wet bottomlands and on dry uplands or on north-facing and on south-facing slopes. Until the limiting factors have been determined experimentally for many more dif-

[1] In a personal communication.

ferent kinds of environment it still appears most desirable to define tolerance in terms of competition.

2. DEFINITIONS OF TOLERANCE

1. Tolerance was originally defined by the Society of American Foresters (1917) as the capacity of a tree to endure shade. Shirley (1945) proposes that the term "shade tolerance" be used to denote "the capacity of a [tree] species to remain alive for long periods in low light intensity." He (1943) suggests that it can be expressed more specifically as the number of years (or months) seedlings will survive in light of 2 to 8 percent intensity.

2. Tolerance is sometimes defined as the capacity of a species or variety for survival, growth, and development under natural canopies of varying degrees of density. This definition recognizes that tolerance is only in part a light relation.

3. In reporting on intensive studies of sample plots in black wattle (*Acacia mollissima*) in South Africa, particularly in Natal, Craib (1934) follows the general lines of the above definition of tolerance, but contends that it refers more appropriately to reproduction under canopies or to understories than to pure, even-aged forest stands. For such stands he proposes that tolerance be defined as the capacity of a species for withstanding competition while still maintaining its growth increment, and particularly its capacity for regaining normal increment after a period of curtailment through overstocking. This definition also recognizes the intense natural competition for growing space (both above ground and below), for light, and particularly for soil moisture and nutrients.

4. More recently the Society of American Foresters (1944) has defined tolerance as *the capacity of a tree to develop and grow in the shade of and in competition with other trees.* In short, it is the capacity of a tree to withstand competition and survive under forest stands. Survival under natural canopies is dependent upon a complex of factors of which light intensity is but one. This definition fully recognizes that, in both fully stocked and overstocked natural forest stands, intense competition occurs for light and growing space above the forest floor as well as for growing space, soil moisture, and soil nutrients below (Korstian and Coile, 1938).

3. METHODS OF DETERMINING TOLERANCE

All methods that have been devised for determining the relative tolerance of tree species may be classified as (1) direct, or (2) indirect.

4. Direct Methods of Determining Tolerance

The direct methods involve either (1) the planting of species under natural forest canopies and the observation of relative vigor and growth after several years, or (2) the observation of relative vigor of natural reproduction of several species under canopies. Planting should be supplemented by seeding in order to determine the relative early survival of the species.

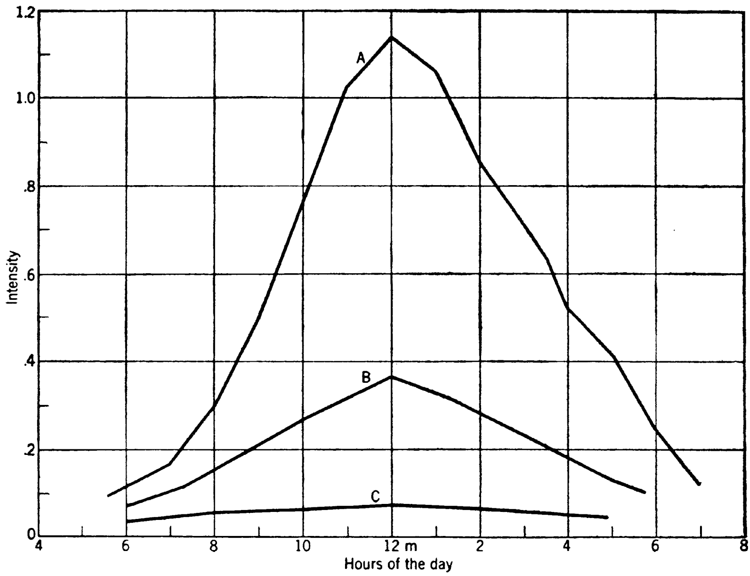


Fig. 19. — Relative light intensities in the open and in the crowns of black locust trees during a clear day — June 10: *A*. Intensity of total daylight in the open; *B*. Within a thin-foliaged crown; *C*. Within a dense-foliaged crown. (*After Wiesner, 1907.*)

The actual light intensities under which trees are growing below natural canopies are commonly measured instrumentally. Evidence thus far available indicates that instruments which measure only the light that is useful to plants are not essential, and that those which measure the non-selective or heating effects of solar radiation are in some respects more desirable. Only those methods which measure the heating effects of solar radiation are uniformly sensitive to all wave lengths and are, moreover, the approved methods used by physicists and astronomers. Gast (1930) has developed a continuously recording

thermoelectric radiometer which obviates the necessity of taking a large number of readings at different points in a forest stand but which requires quite an elaborate set-up of apparatus. Especially for use in forests, Shirley (1930, 1931) has developed a thermoelectric radiometer which is uniformly sensitive to all regions of the solar spectrum, as is the Gast radiometer, and because of its portability offers promise of wider use.

Regardless of the instrument or method used in the direct determination of the light requirements of forest trees, many measurements of light intensity in forests are necessary because light changes with the time of day, season, latitude, altitude, angle between the sun and zenith, relative cloudiness, the interruptions in the crown canopy that admit sun flecks, and even with wind which moves the foliage about in the crown canopy. However, enough data are available to indicate the wide variation in density of natural forest canopies even within the same species (Figs. 3 and 19). Moreover, the greatest variations occur between different species. For example, aspen stands may admit 20 to 25 percent of the total solar radiation whereas only 1 to 2 percent of the total light penetrates dense sugar maple canopies or very dense stands of spruce, fir, or redwood.

5. Indirect Methods of Determining Tolerance

Although the direct methods of determining the relative tolerance of forest trees are most satisfactory, the indirect methods are of some value in indicating relative tolerance. These methods usually involve observations on the anatomical structure and functions of different organs, especially the assimilative organs of trees growing in light and shade. More specifically the observations are concerned with determinations of relative values for some one or more of the following criteria:

1. Density of crown.
2. Number of branch orders.
3. Natural thinning of stand.
4. Condition of reproduction.
5. Relative height.
6. Cambium-crown surface ratio.
7. Artificial shading.
8. Leaf structure.
9. Rate of height growth.

6. Density of Crown. — The density of the crown of a tree is a good indication of its degree of tolerance. The denser the crown, the

less light received by the leaves within it. By this method, in which the crown density is ocularly estimated, the extremes in relative tolerance can be determined with reasonable accuracy, but there is always considerable doubt concerning intermediate species. Actual density of canopy in closed stands is better determined by measurements of light intensity.

7. **Natural Pruning.** — The rapidity with which the lower branches are naturally pruned from the stem of a tree is generally a reasonably good criterion of its relative tolerance. The dying of live branches in the lower portion of the crown may be due mainly to a deficiency of light for assimilation by the leaves and of soil moisture and nutrients. The more intolerant the species and the denser the stand, the more rapid is natural pruning. In fact intolerant species clear themselves of branches in the lower and interior portions of the crown even when growing in the open, although less perfectly than in dense stands. On the other hand, tolerant species lose their lower branches only when grown in dense stands, and in the open the crowns extend down almost to the ground.

8. **Number of Branch Orders.** — If each bud formed on a tree lived and developed into a branch, the tree should contain as many successive branch orders as the tree is years old, minus one. In other words, assuming that during the first year the tree consisted of a single straight stem, the next year each bud developed into a side branch, and the third year these branches in turn produced another set of branches, and so on, the tree when 100 years old would have 99 well-defined sets of branches ranging from small twigs of the last year's growth down to the original stem. This is obviously not the case, because a large number of branches die each year from excessive shading. Thus loss through shading should be greatest in intolerant species and least in tolerant species. The reason for the branches' dying and for many of the buds' failing to develop into branches is found mainly in the minimum light intensities under which the buds and leaves of a given species can develop and function. The development of buds requires higher light intensities than the growth process (Zon and Graves, 1911). Therefore, tolerant species will unfold a proportionately larger number of buds every year and will retain during later life a larger number of branch orders than intolerant species.

Following the logical conclusion that a count of the number of branch orders should indicate tolerance, Wiesner (1907) prepared a list of species based on number of branch orders. In his list the species having the smallest number of branch orders was classed as intolerant and

those with the largest number as very tolerant. The only apparent exception in this list is spruce, which, although actually tolerant, would have to be grouped as intolerant on the basis of number of branch orders. The small number of branch orders in some trees, as spruce, may not be due entirely to light, since many of the smaller branches, twigs, and buds are bitten off by animals, especially squirrels.

Inasmuch as the difference in the number of branch orders between the most tolerant and the most intolerant species is small — rarely in excess of the range from three to eight — interference by animals, insects, and other agencies with the natural formation of successive branch orders constitutes a weakness in this method of determining tolerance. Also the method is probably too complicated for practical use. This method was tried in the eastern United States by DuMond (1922) who found that, although the number of branch orders indicated the relative tolerance for trees with moderate-sized simple leaves, often the number of branch orders is not a satisfactory criterion of tolerance because the number varies with site, age, relative position of the crown in a stand, stand density, diameter of ultimate twig, relative position of branches in the crown, leaf size, and history and treatment of stand, as well as the species. Therefore, he concluded that the preparation of tables of tolerance based on number of branch orders is not warranted because of their inaccuracy.

9. **Natural Thinning of Stand.** — The rapidity with which stands are thinned naturally is sometimes used as a criterion of tolerance (Zon and Graves, 1911). As soon as the crowns in a young stand meet, a struggle for existence follows, which results in the differentiation of dominant and overtopped trees with all the intermediate classes. The trees that lag behind the others in a stand are subjected to increased competition, their growth is retarded, and they become more and more suppressed until finally they die. Thus the number of trees in a stand is gradually reduced, the rate of reduction depending mainly upon the relative tolerance of the species in the stand.

The natural thinning of forest stands is very complex and, although light exerts an important influence upon the process, it has been so difficult to separate fully its effect from that of the other factors that it has remained as a secondary indication of tolerance.

10. **Condition of Reproduction.** — The vigor and condition of reproduction under an older stand, as a criterion of tolerance, has much the same objections as has that of natural thinning, since the extent to which a species can withstand suppression is not determined entirely by its tolerance. This method, although empirical and subject to

personal error in its application, is very commonly used in determining tolerance of trees in the United States (Zon and Graves, 1911).

11. **Relative Height.** — The relation between the height and diameter of a tree varies with the amount of light which it receives. Thus a tree growing in the open is comparatively short and has a large diameter, but a tree in a dense stand is tall and slender. The ratio between the height of a tree and its diameter, obtained by dividing the total height by the breast-high diameter expressed in the same unit of length, has been called its relative height, and actual measurements have clearly shown that it is correlated with the amount of light received (Zon and Graves, 1911).

This method has never come into common use. Although less subjective than some of the other suggested methods of determining tolerance, it rests upon a theory that is uncertain as to whether the distribution of growth in a tree depends entirely, or even mainly, upon light. Moreover, this method is applicable only in fully stocked stands.

12. **Cambium-crown Surface Ratio.** — Although both diameter and height, which are the factors involved in determining relative height, are influenced by the tolerance of a species, Ashe (1915) has suggested that the capacity of a species to withstand crowding of its crown at a given age is a better indication of its light requirements. This may be determined through the ratio between the cambium or growing area and the outer surface or photosynthetic area of the crown of dominant trees. This relationship indicates the proportion of growing tissue on the stem to the chlorophyll-containing crown surface exposed to direct sunlight. In this method the cambium surface of the stem is regarded as the area of a cone, the base of which is equal to the breast-high diameter of the tree inside bark and its height that of the tree, whereas the photosynthetic area is considered as that of a sphere having the diameter of the crown spread. This method has never come into common use. Possibly the measurement of relative photosynthetic efficiency might be a better method.

13. **Artificial Shading.** — Many attempts have been made to determine the relative tolerance of forest trees by growing seedlings under artificial shade. Different criteria have been used to determine the effect of shade, some investigators measuring height growth and others total weight of dry matter produced. In proving that a deficiency of soil moisture in connection with root competition, even under artificial shade, had a pronounced effect upon the results, Burns (1927) showed that this method is generally unsatisfactory for determining tolerance when light relationships are involved.

14. Leaf Structure. — It has already been shown that the structure of leaves developed in the shade is very different from that of leaves grown in the sun. Comparable differences exist between typical leaves of tolerant and intolerant species. The leaves of tolerant trees contain a high proportion of spongy parenchyma; those of intolerant trees have a greater amount of palisade tissue, are thicker, more often leathery, and frequently more densely covered with hairs (Clements, 1905). This criterion of tolerance has not been widely used because of the difficulty of classifying species of intermediate tolerance and because of wide variability within a species under different conditions and in the same tree from top to base of crown and from the outside to its center.

15. Rate of Height Growth. — When tolerant and intolerant trees grow together in full sunlight, Baker (1934) has pointed out that the intolerant trees make more rapid height growth. On the other hand, if the trees are grown under shade the results may be reversed. He shows that the tendency for rapid height growth persists in older trees and that, were this not true, slowly growing intolerant species could not survive in competition with other more tolerant species.

16. FACTORS INFLUENCING TOLERANCE

Tolerance, as well as light intensity, is not always definitely associated with all the other factors of competition. Therefore, Baker (1934) believes that it is useful to distinguish between *real tolerance — the inherent capacity of a tree to withstand competition — and apparent tolerance, which seems to be the tree's ability to survive low light intensities when other growth factors are operative in optimum or near optimum amounts.* Apparent tolerance is markedly influenced by the site factors that affect CO_2 assimilation. The more favorable these factors become, the more able a tree is to withstand shade, its reproduction to survive, and the weaker branches in the crown interior to persist longer.

When apparent tolerance is considered in terms of survival under natural canopies, the tolerance of a given species or variety is found to be extremely variable. It seems to vary with temperature and altitude.

17. Temperature

Plants require less light the higher the temperature and more light the lower the temperature. Therefore the higher the temperature of a locality the more shade a tree can endure. Zon and Graves (1911) point out that this may possibly explain the frequent differences of

opinion regarding the tolerance of the same species when observed in different regions. White pine, for example, can withstand less shade in Maine than in the mountains of northern Georgia. It was a matter of common observation that chestnut survived under denser canopies in Virginia and North Carolina than in New England.

Wiesner (1907) found that while the minimum chemical light intensity as measured by sensitized photographic paper for Norway maple, growing under natural canopies at Vienna, is $\frac{1}{55}$ of total daylight, at Hamar, Norway, it is $\frac{1}{37}$, and at Tromsö, Norway, $\frac{1}{5}$ of full light in the open. Lundegårdh (1930, 1931) concludes that, since the minimum light requirement is reasonably constant for a given species in a given locality, the apparent changes in light requirement with change in altitude and latitude are really due to temperature. Soil temperature rather than direct insolation is probably the significant factor, since it is very intimately related to water absorption by roots (Clements and Martin, 1934).

It has been generally believed that the individuals of a given species, growing in colder latitudes, require fuller exposure to the sun because they require more light for photosynthesis. It is not reasonable to suppose, however, that a tree growing at low temperatures requires more light for photosynthesis, but rather that it requires its specific amount of heat. To maintain suitable soil temperatures the loss in air temperature must be made up by more heat from solar radiation, and for this reason a tree must have fuller exposure to the sun. Many intolerant trees, such as ponderosa pine in Arizona, rarely form dense, closed stands. For such trees much of the heating effect of solar radiation is lost because of wind movement.

18. Altitude

The light requirement of a species increases with increase in altitude up to a certain limit, beyond which it remains constant or even decreases (Zon and Graves, 1911). Wiesner (1907) found that lodgepole pine, at an elevation of 6,400 feet, requires a minimum light intensity of 16.7 percent of full sunlight, whereas at an altitude of 8,500 feet it drops to 15.6 percent and even to 14.5 percent.

The behavior of trees in their extension toward higher latitudes and altitudes is not the same. Zon and Graves (1911) suggest that this is probably due to the fact that the intensity of both direct and diffused light decreases with increase in latitude, and that the light limit of a species is reached when the intensity of total daylight becomes equal to

a tree's minimum light requirement. However, diffused light decreases with increase in altitude, but direct sunlight increases. Hence, with an increase in the intensity of direct sunlight, even though both a decrease in diffused light and a lower temperature occur, the light requirements of a species remain quite constant or even become less at higher altitudes (Fig. 20).

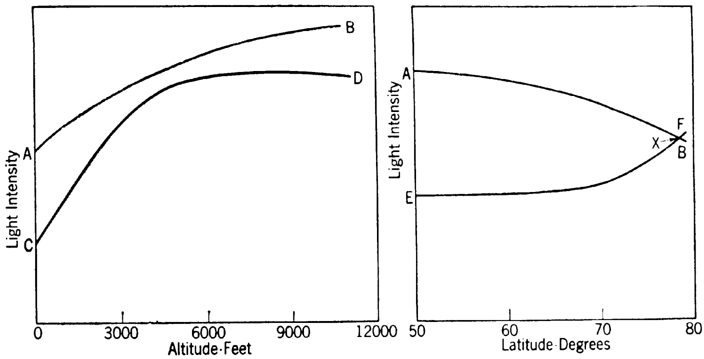


Fig. 20. — Variation in light requirements with increase in altitude and latitude. (*Diagrammatic after Wiesner, 1907.*) *AB*. total light intensity; *CD*. relative light requirements of a species; *EF*. minimum light requirement of a species; *X*. point at which the total light intensity equals the minimum light needed by the species, also limit of latitudinal distribution of the species.

19. SCALES OF TOLERANCE

In silvicultural work it is desirable to have lists of species giving their relative tolerance. Most lists have been developed as opinions following observations based on the criteria of tolerance discussed above. The place of some species in a scale of tolerance is subject to justifiable difference of opinion because of lack of complete agreement between the many criteria of tolerance and because of the variability in tolerance within a given species under the influence of site conditions. Thus, sugar maple (*Acer saccharum*) in the optimum part of its range is very tolerant, particularly so when growing in good soil. In poor soil and under adverse climate it is less tolerant.

Five classes are frequently recognized in a scale of tolerance based on survival, vigor, and growth under living canopies. These classes, ranging from the most tolerant to the least tolerant, are: (1) very tolerant, (2) tolerant, (3) intermediate, (4) intolerant, and (5) very intolerant.

When only three classes are recognized they are: (1) tolerant, (2) intermediate, and (3) intolerant.

General scales of tolerance for the more important species of forest trees indigenous to the United States have been prepared by American foresters. A significant effort in this direction is that of Zon and Graves (1911), who proposed scales of tolerance, segregated for the eastern and western United States. A modification of their scales follows:

EASTERN SPECIES

Very Tolerant

Eastern hemlock (*Tsuga canadensis*)
Balsam fir (*Abies balsamea*)
Southern balsam fir (*Abies fraseri*)
Beech (*Fagus grandifolia*)
Sugar maple (*Acer saccharum*)

Tolerant

Red spruce (*Picea rubra*)
White spruce (*Picea glauca*)
Red maple (*Acer rubrum*)
Southern white cedar (*Chamaecyparis thyoides*)
Black gum (*Nyssa sylvatica*)
Rock elm (*Ulmus racemosa*)
Basswood (*Tilia glabra*)
Sourwood (*Oxydendrum arboreum*)

Intermediate

Red gum (*Liquidambar styraciflua*)
Northern white pine (*Pinus strobus*)
Silver maple (*Acer saccharinum*)
Chestnut (*Castanea dentata*)
White Oak (*Quercus alba*)
Mockernut hickory (*Hicoria alba*)
Shagbark hickory (*Hicoria ovata*)
Southern red oak (*Quercus rubra*)
Black oak (*Quercus velutina*)
Northern red oak (*Quercus borealis*)
Sweet birch (*Betula lenta*)
Yellow birch (*Betula lutea*)
Northern white cedar (*Thuja occidentalis*)
Umbrella magnolia (*Magnolia tripetala*)
Cucumber magnolia (*Magnolia acuminata*)
American elm (*Ulmus americana*)
Sycamore (*Platanus occidentalis*)

Intolerant

Virginia pine (*Pinus virginiana*)
Shortleaf pine (*Pinus echinata*)
Pitch pine (*Pinus rigida*)
Loblolly pine (*Pinus taeda*)
Norway pine (*Pinus resinosa*)
Southern cypress (*Taxodium distichum*)
Black cherry (*Prunus serotina*)
Yellow poplar (*Liriodendron tulipifera*)
Paper birch (*Betula papyrifera*)
Black walnut (*Juglans nigra*)
Pecan (*Hicoria pecan*)

Very Intolerant

Longleaf pine (*Pinus palustris*)
Jack pine (*Pinus banksiana*)
Tamarack (*Larix laricina*)
Black locust (*Robinia pseudoacacia*)
Willows (*Salix spp.*)
Eastern cottonwood (*Populus deltoides*)
Largetooth aspen (*Populus grandidentata*)

WESTERN SPECIES

Very Tolerant

Pacific yew (*Taxus brevifolia*)
Western red cedar (*Thuja plicata*)
Western hemlock (*Tsuga heterophylla*)
Mountain hemlock (*Tsuga mertensiana*)
Engelmann spruce (*Picea engelmannii*)
Alpine fir (*Abies lasiocarpa*)
White fir (*Abies concolor*)

Tolerant

Sitka spruce (*Picea sitchensis*)
Port Orford cedar (*Chamaecyparis lawsoniana*)
Incense cedar (*Libocedrus decurrens*)
Blue spruce (*Picea pungens*)
Redwood (*Sequoia sempervirens*)
Silver fir (*Abies amabilis*)
Lowland white fir (*Abies grandis*)
Noble fir (*Abies nobilis*)
California red fir (*Abies magnifica*)

Intermediate

Douglas fir (*Pseudotsuga taxifolia*)
Bigcone spruce (*Pseudotsuga macrocarpa*)
Alaska cedar (*Chamaecyparis nootkatensis*)
Bigtree (*Sequoia washingtoniana*)
Western white pine (*Pinus monticola*)

Intolerant

Lodgepole pine (*Pinus contorta*)
Jeffrey pine (*Pinus jeffreyi*)
Sugar pine (*Pinus lambertiana*)
Bristlecone pine (*Pinus aristata*)

Very Intolerant

Alpine larch (*Larix lyallii*)
Western larch (*Larix occidentalis*)
Whitebark pine (*Pinus albicaulis*)
Knobcone pine (*Pinus attenuata*)
Foxtail pine (*Pinus balfouriana*)
Coulter pine (*Pinus coulteri*)
Limber pine (*Pinus flexilis*)
Ponderosa pine (*Pinus ponderosa*)
Singleleaf piñon (*Pinus monophylla*)
Piñon (*Pinus edulis*)
Digger pine (*Pinus sabiniana*)

Local scales are more useful and of much more silvicultural importance than are general scales of tolerance. The following is a local scale for the more important economic species in southern Connecticut:

Very Tolerant

Eastern hemlock (*Tsuga canadensis*)
Beech (*Fagus grandifolia*)
Sugar maple (*Acer saccharum*)
Blue beech (*Carpinus caroliniana*)
Hop-hornbeam (*Ostrya virginiana*)
Dogwood (*Cornus florida*)

Tolerant

Black gum (*Nyssa sylvatica*)
Basswood (*Tilia glabra*)
Red maple (*Acer rubrum*)

Intermediate

Northern white cedar (*Thuja occidentalis*)
American elm (*Ulmus americana*)
Northern white pine (*Pinus strobus*)
Sweet birch (*Betula lenta*)
Yellow birch (*Betula lutea*)
Swamp white oak (*Quercus bicolor*)
Red oak (*Quercus borealis*)
Black oak (*Quercus velutina*)

Sycamore (*Platanus occidentalis*)
White ash (*Fraxinus americana*)
Chestnut (*Castanea dentata*)

INTOLERANT

Black walnut (*Juglans nigra*)
Scarlet oak (*Quercus coccinea*)
White oak (*Quercus alba*)
Chestnut oak (*Quercus montana*)
Mockernut hickory (*Hicoria alba*)
Shagbark hickory (*Hicoria ovata*)
Butternut (*Juglans cinerea*)
Yellow poplar (*Liriodendron tulipifera*)
Black cherry (*Prunus serotina*)

VERY INTOLERANT

Eastern red cedar (*Juniperus virginiana*)
Tamarack (*Larix laricina*)
Aspen (*Populus tremuloides*)
Largetooth aspen (*Populus grandidentata*)
Gray birch (*Betula populifolia*)
Black locust (*Robinia pseudoacacia*)

20. SILVICULTURAL IMPORTANCE OF TOLERANCE

Knowledge of the relative tolerance of different forest-tree species is essential in silvicultural practice. Many rules have been formulated and practices developed which are based upon the relative tolerance of trees and stands. Prior to the time of Fricke (1904) these rules and practices were predicated almost entirely upon the assumption that tolerance was a very simple reaction to light instead of the result of reactions to a complex of factors, which includes the characteristics of seed and seed bed, the basal metabolism of the different species, as well as the basic requirements for light, soil moisture, and soil nutrients, and freedom from severe browsing and insect attack. However, many of the older rules are still applicable, because competition, even in its strictly modern, more inclusive sense, varies about the same as competition for light alone.

In European forestry practice special emphasis has been laid upon the undesirable effects of open stands of intolerant species. In fact pure stands of intolerant species were generally considered so undesirable because of the deleterious effects of insolation and drying winds on the surface soil that such stands were commonly underplanted with tolerant species (Nisbet, 1894). Mixed stands of tolerant and intol-

erant species were strongly advocated because of the beneficial effects of the tolerant species in protecting the surface soil from the sun and wind and in maintaining or increasing productivity of the soil. Only those species, which have dense crowns and grow in stands with closed canopies, such as beech, spruces, and firs, were advocated to be grown in pure stands. It was considered permissible to grow the open-crowned intolerant pines in pure stands as long as they had a mossy ground cover to protect the surface soil.

The early recognition of tolerant and intolerant trees and of the necessity for different silvicultural treatments depending upon their relative reactions to light was due mainly to Gustav Heyer (1852). The extent to which the early concept of tolerance, then regarded as only a reaction to light, influenced silvicultural management is shown by the following principles, originally formulated soon after the results of Heyer's basic studies were published (Heyer and Hess, 1906, 1909):

1. The predominant species should be grown in mixtures capable of improving the soil.
2. Shade-tolerant species may be grown in mixture with each other when their rate of growth is about equal or when the more slowly growing species is protected against the more rapidly growing species.
3. Dense-crowned, shade-tolerant species can be intermixed with open-crowned, light-demanding species, when the latter either grow more rapidly in height or are afforded some advantage as to age or height.
4. Light-demanding species should not be associated in permanent mixtures.
5. The subordinate species should generally be distributed singly or only in small groups of 3 to 5 stems and not in thickets under the dominant species.

These older silvicultural principles are indicative of the then existing apprehension over the possible adverse effects of sunlight and drying winds unless a forest was kept dense and apparently moist. Baker (1934) points out that they indicate how little the effect of root competition for soil moisture was appreciated. The beneficial effect of under-planting the intolerant pines with tolerant beech, which has been done extensively in Europe, lies not so much in retaining available soil moisture as in maintaining conditions favorable for nitrification. The continued maintenance of overly dense stands under which there is little or no herbaceous vegetation for decade after decade has led to extensive soil deterioration and even to podsolization in some forests.

It is very essential that tolerant species be so managed in mixed stands that they will not gain the ascendency over desirable intolerant trees, or else the latter will be eliminated from the stand unless they are favored by proper methods of cutting, thinning, or other treatment

(Baker, 1934). Tolerant species are capable of survival and growth for relatively long periods as subordinates in the understory; but intolerant species must grow rapidly enough to keep their crowns well up in the overstory, or else they will succumb to the intense competition of the tolerant trees whenever these become more aggressive than the intolerant species.

CHAPTER XVII

FOREST VEGETATIONAL UNITS AND THEIR CLASSIFICATION

1. CONCEPTS

With the constantly increasing utilization of forest products of the world has gone a rapid development in the study of trees and other forest plants in relation to their natural environment. One of the earlier phases of the study was the compilation of floras and their employment in plant geography and in ordered knowledge of the floristic regions of the earth. These studies were largely confined to the distribution of species in reference to the floristic affinities of regions. Upon these earlier studies in floristic plant geography has been imposed the study of the natural assemblages of plants, that is, plant communities of varying degrees of magnitude.

Modern forest ecology is primarily the study of the relations between tree populations, as functioning organisms, and environments as physical complexes. Silviculturists are not only concerned with the collective activities of a tree as controlled by environment but they are even more concerned with the assemblages of trees and other forest plants which occupy natural situations or sites. Forest geography which is primarily descriptive of the vegetation has an extensive literature, but the physical complex which makes up the environment has a fragmentary and meagre literature. Studies of the physical complex and the physiological responses are essential if quantitative relations are to be established between vegetation characteristics on the one hand and environmental conditions on the other.

2. Cause and Effect

Forest vegetation is the response to the various site factors operating as a physical complex and supplementing each other. The physical complex is the cause and the forest vegetation is the effect. Forests, in turn, act upon and modify the physical complex. As the combined influence of site factors is different in one place as compared with another, the resulting vegetation exhibits corresponding differences. It is, therefore, possible to recognize rather well-defined vegetational areas and plant communities. These communities occupy areas throughout

which the intensity and duration of action of the site factors are reasonably uniform. Warming (1909) states that the different factors can not be regarded separately, because a plant community is the product of all. Climate alone can not account for the many different forest communities, each differing from the others in one or more respects. Neither can differences in soil account for them. Some plant communities are largely determined by climate, others by physiography. Where the ground is level and the soil of uniform depth and fertility, a single community of a given magnitude often extends over a relatively large area and is continuous. Owing, however, to differences in topography, plant communities of all magnitudes are usually discontinuous. In other words, a single community seldom extends over a large area without being interrupted by other communities, no matter how uniform the climate. Furthermore, the same community may reappear in somewhat different climates where physiographic conditions compensate for differences in climate. Thus along stream bottoms in the plains, increased soil moisture compensates for low precipitation and topography creates locally an environment differing from the habitats of the general region.

3. Classification of Vegetation

The observation, description, and classification of vegetation areas and plant communities have been under way for many years. For the most part, however, the attempts to classify and delimit these areas and communities have resulted in much disagreement among authors and, as a consequence, many classification schemes have been prepared for general application (Livingston and Shreve, 1921).

The great difficulties inherent in the classification of vegetation into units of varying degrees of magnitude based on the interrelations between vegetation and the physical complex have led authors to base their classifications on the physical characteristics of site alone, or on the apparent differences in vegetation as expressed in growth forms. Other classifications are based partly on site characteristics and partly on vegetational characteristics.

When the vegetation on two areas, widely separated geographically, is physiologically alike, it is logical to classify the areas together. When physiological differences are discernible they should form the basis for separation. Furthermore, physiological differences, particularly those relating to water requirements, are most strikingly expressed in growth form rather than in taxonomic relationships. Although most plants that form the characteristic vegetation of different

vegetational areas are physically controlled, there may be relict species among the dominants at any given time which are not perfectly adjusted to the physical environment and are disappearing. On the other hand, there may be recent species among the dominants which are very abundant. In general, however, it may be said that plants which make up the dominants in our natural vegetation have their distributional limits imposed by physical factors now operative or which have been operative in the immediate past.

When the many, diverse growth forms, irrespective of taxonomic relationships, are arranged in a classification in accordance with their physiological affinities, species have been brought together which are widely divergent taxonomically but nevertheless have made the same successful adjustments to their environment.

4. Classification of Vegetation on Basis of Growth Form. — A large number of classifications of vegetation on the basis of growth form has been made, beginning with the simple classification by Humboldt (1805). Following the earlier classifications are the more extensive ones of Drude (1890), Warming (1909), Du Rietz (1930), and Raunkiäer (1905, 1934) abroad and Pound and Clements (1900) in this country. Although the system proposed by Raunkiäer has received much attention, Drude's (1913) carefully elaborated system of growth forms is the most complete and also the most natural in that it ignores phylogenetic distinctions. Although the various systems proposed are widely divergent, when one examines the criteria upon which the various classifications are based it appears that water relations are of paramount importance. In a few proposals for classification, notably those by Merriam (1894), Brockman-Jerosch (1919), and Livingston and Shreve (1921), some importance has been attributed to temperature in limiting the distribution of species and vegetation.

5. Natural Vegetational Areas

Trees and other plants which grow together naturally form plant communities occupying natural vegetational areas. The study of vegetation in contrast to the study of individual plants is concerned with phenomena exhibited by plant aggregates as distinguished from those exhibited by the individuals comprising the aggregates. When vegetation is examined one finds that vegetational areas are of varying degrees of magnitude and have varying spatial relationships. Also one finds that plant communities which occupy them are of varying degrees of magnitude depending on the degree of divergence in physiological

characteristics as expressed in growth form, which is determined by the environment.

The study of vegetation has resulted in the recognition of different degrees of community existence among plants, correlated with degree of divergence in the physical characteristics of the environment. Different names have been employed to represent vegetational areas and vegetational units classified upon different bases. In general these names relate to geographical position, such as region and district, or to the vegetation itself, such as desert, grassland, and forest, with their various subdivisions based on growth forms. The geographical classification is artificial, in that unrelated and unlike growth forms may appear as dominants in the same unit. The vegetation classification is natural in that the aim is to bring together in each unit dominant plants having the same physiological requirements. None of the terms employed appear to be used by authors in precisely the same sense; hence, there is, as yet, no general agreement in the classification and nomenclature of vegetation.

6. FOREST VEGETATIONAL AREAS IN UNITED STATES

All forest geographers recognize the existence of a number of forest vegetational areas in the United States. These areas have been delimited on widely different bases, which may be considered under two broad groups: (1) From non-ecological, and (2) From ecological standpoints.

7. Forest Vegetational Areas on a Non-ecological Basis

8. Brewer's Classification. — Brewer (1874) prepared a map of the United States showing distribution and density of American forests in connection with an analysis of our forest resources. He divided the forests of the country into 10 regions based entirely on political divisions, irrespective of both floristics and growth forms. His map shows the distribution of forests in five degrees of density in the 10 recognized regions as follows: (1) New England; (2) The Middle States; (3) The Southeastern Region; (4) The Northwestern Region; (5) The Southwestern Region; (6) Plains Region; (7) Rocky Mountain Region; (8) Arizona, New Mexico, and the Great Basin; (9) Pacific Region; and (10) Alaskan Region. This map is now of little more than historical interest.

9. Sargent's Classification. — Sargent (1884) prepared the first comprehensive report on the distribution of forests in the United States. The report was accompanied by numerous maps showing distribution

of species and genera, relative density of existing forests, and natural divisions of forests of the country. The basis for the separation of forests into " natural divisions " was primarily floristic, although it was recognized that the causes which produced dissimilar vegetations must be sought " in climatic conditions and topographical distinctions." Sargent recognized the Atlantic and Pacific regions. He classified forests in the Atlantic region under 6 natural divisions: Northern forest, northern pine belt, southern maritime pine belt, deciduous forest of the Mississippi basin and the Atlantic plain, the semi-tropical forest of Florida, and the Mexican forest of southern Texas. The 4 western divisions included: The northern forest, coast forest, interior forest, and Mexican forest. The 10 divisions of forests of the United States as mapped by Sargent differ radically from the 10 regions delimited by Brewer. While Brewer's divisions were based on political boundaries, Sargent's were based primarily on floristics. He says, " These natural divisions, although composed in part of species found in other divisions, and possessing many general features in common, are still, for the most part, well characterized by predominant species or groups of species, making such a separation natural and convenient." Although growth form is not considered in his classification, his divisions tend toward a natural classification, because political boundaries are ignored and the distribution of individual species is subordinated to predominant species and groups which give the forest in each division a more or less distinct physiognomy. For the above reasons Sargent's map although based on floristics, is not strikingly different from later maps on which the delimiting of larger vegetational areas has been based on growth forms. Sargent, in his description of the 10 major divisions of the forests of the United States, emphasizes the correlation of rainfall, temperature, and other climatic factors as well as physiographic features, particularly topography and soil, with the particular vegetation of each division.

10. **Merriam's Classification.** — From the study of the geographical distribution of native plants and animals, Merriam (1894) established 7 transcontinental belts and a number of minor areas, each of which is adapted to particular associations of animal and plant life. He divided the continent of North America into 3 primary transcontinental areas in accordance with the distribution of animals and plants and called them Boreal, Austral, and Tropical. He found that the flora and fauna within each of these areas are not homogeneous but " characterized by particular associations of animals and plants." In order to conform with these particular associations he divided each

of the primary areas into a number of minor belts or areas. Thus the Boreal was divided into the Arctic, Hudsonian, and Canadian and the Austral into the Transition, Upper Austral, and Lower Austral. The Tropical, although capable of division, was left undivided because it reaches the United States only in the extreme southern parts of Florida and Texas. These divisions were termed life zones. The flora and fauna of each life zone and of each important subdivision were described. In the mapping of these zones, temperature was assumed as the most important single factor in fixing the limits beyond which particular species of plants and animals can not go. From Merriam's studies of distribution he concluded that "the northward distribution of terrestrial animals and plants is governed by the sum of the positive temperatures for the entire season of growth and reproduction and that the southward distribution is governed by the mean temperature of a brief period during the hottest part of the year." In computing the sum of the positive temperatures he assumed a minimum temperature of 43° F. as marking the inception of the period of physiological activity in plants and of reproductive activity in animals. Normal daily means in excess of this minimum were added from the beginning of the season until the end and the sums thus obtained were plotted on an outline map of the country and connected by isotherms. These lines were found to conform reasonably well with the northern boundaries of the several life zones laid down.

The mean normal temperature for the 6 hottest weeks at each station was arbitrarily chosen and the sum of the positive temperatures plotted as before. Isotherms drawn from this data conformed with the southern boundaries of the Boreal, Transition, and Upper Austral zones.

Although the system of life zones worked out by Merriam appears to show a very close correlation of biological areas (based on distribution of certain species) with the temperature factors employed, climatic maps showing these temperature factors were employed as the basis in the original form of the life zone map (Livingston and Shreve, 1921).

11. **Mayr's Classification.**—Mayr's division of forests of the United States into zones on the basis of climatic factors appears to be the first attempt on the part of a forester to correlate forest vegetational areas with certain site factors. Mayr (1925) states that the climatic factors, air temperature and humidity, play the most important rôle in accounting for the presence or absence of forests. He considers the average temperature for the 4 main months in which plant growth occurs, namely, May, June, July, and August, the chief factor in determining the limit of forest extension in the northern hemisphere

when moisture conditions are suitable. Wherever the mean air temperature during this period is below 50° F., no forest exists. The climatic data upon which Mayr's classification is based are: Average temperature during the 4 hottest months, mean annual temperature, first frost in the autumn, last frost in the spring, and the lowest recorded temperature. Based upon the above data, Mayr recognizes the following forest zones in North America, each of which is divided into the Atlantic, Central, and Pacific regions:

1. The polar-alpine zone — the cold area of stunted and dwarfed trees at the limits of forest growth.
2. The spruce, fir, and larch zone — the moderately cold area of spruces, firs, and larches.
3. The beech zone — the cooler half of the temperate area of deciduous species.
4. The chestnut zone — the warmer half of the temperate area of deciduous species.
5. The laurel zone — the subtropical area of evergreen oaks and laurels.
6. The tropical zone — not represented in the United States.

The many efforts made to delimit natural vegetational areas on the basis of temperature relations have come to naught, because of the extremely weak correlations that have as yet been discovered between growth form and temperature. One can not go into a region and from the vegetation itself classify it on the basis of temperature requirements. A vegetation of low temperature requirements can not be distinguished from one of high. It is for this reason that a natural classification rests so largely on water relations, which make a very striking and recognizable imprint on the vegetation. The main shortcoming of all the early attempts at the classification of forest vegetation was the impossibility of explaining distribution on the basis of a single factor. These early attempts did not recognize that forest environments are a resultant complex of the interaction of many site factors, several of which, in turn, become significant.

12. United States Forest Service Classification. — It has been the practice of the U. S. Forest Service to consider the forest vegetation within the continental United States as embraced in 6 forest regions (Mattoon, 1936). The boundaries of these regions have been more or less arbitrarily drawn, and consequently unrelated kinds of forests appear in each. They are not delimited from physiological characteristics as related to distributional features but rather from floristic characteristics. It is obvious, however, that genetic relationships bear little relation to growth forms. Often a dozen or more growth forms appear in the same family; on the other hand, a single growth form

may appear in many families widely separated phylogenetically. In the main, however, the dominant species characteristic of a given area have the same growth forms, as illustrated in the dominant small-leaved or leafless woody vegetation of southern Arizona and the large-leaved deciduous, woody vegetation that forms the dominant vegetation of Indiana.

The 6 forest regions recognized by the U. S. Forest Service and herein described include not only areas covered with tree vegetation but also denuded areas and to some extent chaparral areas of low woody vegetation. They may be briefly described as follows:

1. *The northern forest* lies chiefly north of the United States. Within the United States it is mostly in the Lake States, New England, and in New York and Pennsylvania. A strip continues along the Appalachian Mountains to northern Georgia. The climate is moderately cool with the precipitation well distributed over the year. The northern forest is characterized by red, black, and white spruces, balsam and southern balsam firs, white, Norway, jack, and pitch pines, hemlock, sugar and red maples, beech, northern red, white, black, and scarlet oaks, yellow, paper, black, and gray birches, aspen, largetooth aspen, basswoods, black cherry, white and black ashes, northern white cedar, and tamarack.

2. *The central hardwood forest* is chiefly in the interior states. It abuts on the prairies of the Great Plains from Canada to Mexico and extends eastward over the drainage of the central Mississippi and Ohio rivers, reaching the coast in southern New England to New Jersey. The climate is variable over its various parts. Precipitation is evenly distributed over the year in the east but becomes more and more restricted to the growing season in the west. This forest is characterized by a great variety of trees, for the most part broadleaved deciduous species. It is, however, by no means confined to broadleaved species. Red cedar reaches its best development therein. Chestnut is an element in its eastern part; white, black, northern red, scarlet, bur, chinquapin, and chestnut oaks, shagbark, mockernut, pignut, and bitternut hickories, white, blue, green, and red ashes, American, rock, and slippery elms, red and silver maples, beech, sycamore, black walnut, cottonwood, black locust, and eastern red cedar are elements in its northern part; white, post, southern red, blackjack, Shumard red, pin, swamp chestnut, and chestnut oaks, red and black gums, mockernut, pignut, southern shagbark, and bigleaf shagbark hickories, shortleaf and Virginia pines, yellow poplar, green, white, and blue ashes, winged, American, and red elms, sycamore, black walnut, silver and red maples,

dogwood, persimmon, swamp and eastern cottonwoods, eastern red cedar, and holly in its southern part; and elms, cottonwood, ash, and walnut in its western part.

3. *The southern forest* is chiefly in the southern Atlantic and Gulf states. It extends as far north as southern New Jersey in the east and southern Missouri in the west. The climate is moderately warm with but little snow in winter. The precipitation is uniformly distributed over the year. This forest is characterized by longleaf, shortleaf, loblolly, and slash pines, southern red, turkey, black, post, laurel, and willow oaks, red gum, winged, American, and cedar elms, black, red, sand, and pignut hickories, eastern and southern red cedars, and pond and sand pines on the pine land; and red, tupelo, and swamp black gums, water, laurel, live, overcup, Texas red, and swamp chestnut oaks, southern cypress, pecan, water, swamp pignut, and hammock hickories, beech, river birch, water, green, pumpkin, and white ashes, red and silver maples, cottonwood, willows, sycamore, sugarberry, honey locust, holly, red and sweet bays, evergreen magnolia, pond and spruce pines, and southern white cedar in the hardwood bottoms and swamps.

4. *The Rocky Mountain forest* extends over the Rocky Mountain system from Canada to Mexico; west into the interior desert basin and east to the Great Plains. It touches the Pacific forest in the extreme northwest; otherwise it is surrounded and broken into many parts by grassland vegetation to the east and desert vegetation to the west. This forest is chiefly confined to high elevations with moderately cool climate, but with hot days during the growing season. Precipitation is extremely variable and unevenly distributed over the year. This forest is characterized by conifers, particularly in the central and southern parts, by ponderosa, lodgepole, limber, bristlecone, Mexican white, and Arizona pines, piñon and singleleaf piñon, Englemann and blue spruces, Douglas, white, alpine, and corkbark firs, Rocky Mountain red cedar, and one-seeded, alligator, and Utah junipers. In the northern part of this region some of the species of the northern Pacific coast forest are associated with many of those common to the central part of the region.

5. *The Pacific coast forest* extends through all the Pacific coast states and in the north reaches eastward through northern Idaho into western Montana. North of the United States it extends into Alaska. Like the Rocky Mountain forest, its greatest extension is north and south; hence its different parts are extremely variable in climate, particularly in temperature and precipitation. For the most part the

distribution of precipitation is extremely uneven, the larger part falling during the winter season. The northern part of this forest is characterized by an extremely heavy winter precipitation and a long cool growing season. The soil is almost entirely of porous gravel variable in depth, and it is largely of glacial origin. This forest is characterized by many superb conifers but by few hardwoods. The conifers include Douglas, lowland white, noble, and silver firs, western and mountain hemlocks, western red, Port Orford, and Alaska cedars, Sitka and Engelmann spruces, western white and lodgepole pines, and western and Lyall larches. Black cottonwood is the most imposing broadleaf species. The southern part of this forest, extends from the Shasta region in northern California to Lower California and is much more truly a mountain forest than is the northern part. The growing season is much warmer and drier. Precipitation decreases southward. This forest is also characterized by conifers, there being few hardwoods. The conifers include ponderosa, sugar, Jeffrey, lodgepole, knobcone, and digger pines, Douglas, white, red, and lowland white firs, redwood, bigtree, incense cedar, bigcone spruce, western and California junipers, and singleleaf piñon.

6. *Tropical forest* within the United States is limited to the coast in extreme southern parts of Florida and Texas. The summers are hot and the winters mild. Precipitation is uniformly distributed over the year. This forest is composed of many species of hardwood trees, most of which are small and bear evergreen leaves and pulpy berries or stone fruits (Mattoon, 1936). These species represent the northernmost extension of their natural ranges, which mostly include at least part of the West Indies, Central America, and even South America. This forest is characterized principally by mangrove, royal and thatch palms, wild fig, pigeon plum, blolly, wild tamarind, gumbo limbo, poisonwood, inkwood, buttonwood, mastic, and Jamaica dogwood.

13. Forest Vegetational Areas on an Ecological Basis

When the forests of the country are considered from an ecological standpoint and studies are based on the physiological characteristics of the plants composing them, in their relation to distributional features, it is at once evident that phylogenetic relationships are relatively unimportant. Obvious differences between plants expressed in growth forms rather than differences in phylogeny form the criteria for a natural classification, because the growth forms bear a direct relation to the physical factors of the environment.

Much attention has been given recently to describing distinct

types of plants (anatomically and physiologically) under the name of growth forms. The recognition of growth forms is an effort to establish a classification into which all the various types that plant life has assumed, as an adaptation to environment, can be placed. Because the significance of all growth forms from a physiological standpoint are not known the classification of vegetation on this basis is as yet imperfect.

A number of plant ecologists have classified the forest vegetation of the United States in recent years purely from a vegetational standpoint. These classifications are of unusual importance to foresters because they recognize the relation of cause to effect in forest distribution. The application of modern plant ecology to silviculture finds recognition in the recent writings of Düesberg (1910), Wagner (1923), Mayr (1925), Rubner (1934), and Dengler (1935). Schimper's (1903) subdivision of vegetation into *forest, grassland,* and *desert* is a natural division based purely on vegetational criteria. Most recent authors have followed Schimper in the broad divisions of vegetation, but there is much disagreement in the further subdivision into natural units of lesser magnitude. As defined by Schimper, forests are composed essentially of ligneous plants, grassland of perennial grasses, and desert vegetation of both ligneous plants and grasses stunted by adverse climate and growing in open stands.

The forests of the world are distributed over those portions of the earth where the combined influence of the site factors falls within certain but as yet imperfectly known limits. In the main the portions of the earth that are naturally covered by forests are determined by climate and to a lesser extent by physiography. The climatic requirements of forest are very different from those of grassland and desert, and this is particularly true as relates to precipitation. In forest vegetation the transpiring surface is a greater distance from the water supply in the soil than in grassland and desert vegetation, and the surrounding strata of air differ in many respects from those nearer the ground. The transpiring surface exposed to the air in a forest is usually much larger than the surface exposed by grassland or desert vegetation for an equal land area. Forest vegetation not only uses more water than grassland vegetation, but sometimes it is also obtained in part from much greater depths. The depth and extent of the root systems of some trees make it possible for them to thrive where long seasons of drought occur periodically. Neither frequent atmospheric precipitation nor wet growing seasons are necessary for forest vegetation, but it is necessary that there be a continuous supply of available water in the soil

within reach of the absorbing rootlets. The distribution of precipitation over the growing season as well as the amount of annual precipitation is important. It is rather immaterial when the yearly supply is renewed, so long as the soil moisture does not become exhausted, not only during the growing season, but during the winter season as well. When forest vegetation occurs in a region which has a dry growing season, as in the mountains of California, it depends on water collected in the ground at other seasons and retained at considerable depth. The root systems of the elements composing the vegetation must be deep seated. On the other hand, when forest vegetation occurs in a region where precipitation is uniformly distributed over the year, the surface layers of soil are not subject to excessive drying and consequently the root systems are not so deep seated. Forests thrive well in regions with little rain during the growing season, and in regions where precipitation is uniformly distributed over the year, provided there is sufficient annual precipitation to keep the deeper layers of the soil adequately moist at all seasons.

Grassland vegetation on the whole, as compared with forest vegetation, is composed of more shallow-rooted elements; consequently moisture in the deeper layers of subsoil has less influence upon it. It is the moisture in the upper layers of soil that is of fundamental importance. An average annual precipitation of 20 to 30 inches, with 80 to 90 percent falling in December, January, February, and March, produces forest in the mountains of California, whereas the same annual precipitation, with 70 to 85 percent falling in April, May, June, and July, produces grassland on the loess soils of Kansas and Nebraska and even in the sandhill region of Dakota and western Nebraska.

In the transition zone between woodland and grassland and between woodland and desert the rate of air movement is of importance, because of the height of woodland vegetation above the ground. High winds combined with intense cold determine the timber line on mountains, and not great cold alone. High altitudes in a climate with dry winters and little snow are hostile to forest vegetation because, when the ground is solidly frozen by the severe cold, trees cannot replace water lost through winter transpiration. Relative humidity of the air influences forest vegetation much more than grassland vegetation because its transpiration surface is less favorably situated. Middendorf (1853) has shown that in temperate regions, coast districts sustain a more abundant and luxuriant tree vegetation than interior districts, owing to the much greater dryness of air in interior regions, particularly during the winter.

An ideal forest climate has a moderately warm growing season, a

moist subsoil at all seasons, and damp, calm air, particularly in winter. Dry winters are harmful to forest vegetation because trees can not replace by absorption moisture lost through transpiration. An ideal grassland climate has frequent precipitation during the growing season, a moist surface soil and a moderate amount of heat. Dry winters do little harm, but drought during spring or early summer is unfavorable.

14. Clements' Classification. — Clements (1916) has recognized 9 subdivisions of large magnitude in the forest vegetation of the United States. They are differentiated on the basis of growth forms and climates and are as follows:

1. Boreal: Picea-Abies forest.
2. Lacustrian: Pinus forest.
3. Deciduous: Acer-Fagus forest.
4. Coastal: Pinus forest.
5. Mesa: Juniperus-Pinus forest.
6. Mountain: Pinus-Pseudotsuga forest.
7. Alpine: Picea-Abies forest.
8. Pacific: Thuja-Tsuga forest.
9. Insular tropical forest.

15. Shreve's Classification. — Shreve (1917) has compiled a map of the vegetation of the United States in which he has based the subdivisions and boundaries entirely on vegetational criteria with entire disregard of climatic, physiographic, geological, floristic, and historical considerations. The vegetational criteria used were partly features of physiological behavior and partly features of anatomical structure. The latter were used because they are outward indices of physiological behavior. Only the largest features of difference between plant communities were considered in order to segregate those that possess marked features of dissimilarity in the gross physiological character of their dominant plants. The vegetation considered in each locality was the predominant plant covering of average upland. It was found exceedingly difficult to draw hard and fast lines between communities which intergrade very gradually from one to the other. In such communities transition areas were recognized. The natural vegetational areas recognized merely represent the most natural subdivisions of the vegetation from a physiological standpoint as conceived by Shreve. The nomenclature employed avoided terms that relate to site factors, floristics, and morphological distinctions but involved those which primarily describe the character of vegetation and indicate its geographical location.

Shreve followed Schimper's primary subdivision of vegetation into

forest, grassland, and desert. He recognized and characterized 18 vegetational areas which he delimited on a map. Of these areas 10 are forest in whole or in part and the remainder, grassland and desert. The forest vegetational areas are briefly described as follows:

1. *Grassland-deciduous forest transition.* — The rather ill-defined belt in which the deciduous forest emerges from floodplains and river margins and occupies a portion of the upland. On the western edge of the belt there is a high percentage of grassland; in the eastern portion the deciduous forest becomes nearly continuous. The principal trees of this region are bur, white, and black oaks; the principal grasses, beard grass, Indian grass, and dropseed.

2. *Deciduous forest.* — The extensive area in the Mississippi Valley and southern Appalachians which was formerly occupied by an almost unbroken forest of 50 or more species of deciduous trees. A few prairies occur in the southern portion of the area, and conifers occupy bluffs and shallow soil in the mountains. The commonest trees are species of oak, hickory, chestnut, beech, maple, walnut, yellow poplar, and ash.

3. *Southeastern evergreen-deciduous transition forest.* — The area in which there is a nearly equal commingling of deciduous and evergreen species of adjacent regions. Local bodies of purely deciduous or purely evergreen forest are determined by soil and physiographic conditions. The commonest evergreen trees are loblolly, shortleaf, and Virginia pines, and the commonest deciduous trees are post, Spanish, and bluejack oaks.

4. *Southeastern mesophytic evergreen forest.* — The coastal plain forest of evergreen coniferous trees with a subordinate admixture of evergreen, broadleaved and deciduous species. Extensive areas of this forest are pure longleaf pine or slash pine in open stands with the forest floor nearly devoid of shrubs and carpeted with grasses and herbaceous plants.

5. *Northeastern evergreen-deciduous transition forest.* — A region in which trees of the deciduous forest area and those of the eastern portion of the northern mesophytic evergreen forest are intermingled in nearly equal proportions. A very common type of forest in this region is that in which maple, beech, and hemlock are dominant.

6. *Northern mesophytic evergreen forest.* — This extensive region is characterized throughout by a pure or nearly pure stand of evergreen conifers, among which deciduous trees are often present either as minor components of the forest or as an understory. Virgin stands of this forest range from 60 to 125 feet in height and vary from open park-like

formations to heavy forest with a completely shaded floor. The heavier stands are almost devoid of shrubby undergrowth, but the more open ones are accompanied by deciduous shrubs and understory trees. In spite of the essential identity of this forest from the Pacific to the Atlantic it is made up of a large number of tree species. Very many extensive areas are covered by a single species and many others by an admixture in which not more than three or four species are involved. In the western half of the area ponderosa pine, lodgepole pine, and Douglas fir dominate the most extensive stands. In the eastern portion of the area white pine, hemlock, red and white spruces, jack pine, and balsam fir are the most common species.

7. *Western xerophytic evergreen forest.* — An open forest of low stature, the trees seldom exceeding 40 feet in height. The conifers are dominant, but this forest is everywhere accompanied by shrubs and by some succulent or semi-succulent plants, and the floor is carpeted in many localities by an open growth of perennial grasses. Along the Mexican boundary this forest merges into the encinal, or evergreen oak type. The dominant species of the xerophytic evergreen forest vary from region to region but are almost always either junipers or piñon pines.

8. *Northwestern hygrophytic evergreen forest.* — A well-marked type of forest characterized by density of stand and by size of trees, which commonly reach 100 to 125 feet in height and often exceed 250 feet. The forest floor is heavily shaded and supports relatively few deciduous understory trees, although there is usually a rich growth of shrubs, mosses, and other herbaceous plants. The trees which characterize this area are firs, hemlocks, redwood, and western red cedar.

9. *Alpine summits.* — Portions of the higher mountains which lie just below timberline, characterized by a very scant growth of stunted or prostrate trees, by mats of alpine herbaceous plants, or merely by mosses and lichens.

10. *Swamps and marshes.* — The swamps support evergreen and deciduous trees in great variety, southern cypress and tupelo gum being the commonest trees in the southern swamps. The marshes are widely varying areas of grasses, sedges, and emersed aquatic plants.

16. Zon's Classification. — Shantz and Zon (1924) have classified and mapped the natural vegetation of the United States. Shantz classified and mapped grasslands and desert vegetation and Zon, with the assistance of certain other members of the U. S. Forest Service, the forest vegetation. No attempt was made to correlate the vegetation with climatic or other physical factors. They accepted the natural

vegetation itself "as a better basis for the classification of environments than any one site factor or set of factors." Vegetational units were described and mapped not as aggregations of species but as communities characterized by certain similarities in their biological aspect. These biological units are the basis of classification and their environments are measured in terms of vegetation and not in terms of temperature or other site factors. The basis for classification and mapping is practically identical with that of the earlier work by Shreve. The authors appreciate that on a small scale map, because of the lack of abrupt vegetational changes, the plant cover, particularly on the borderland between two types, might be classified differently by different persons. Furthermore, owing to the generalized character of the map the vegetation as represented does not necessarily correspond with the details of vegetation cover as it actually exists. The vegetation considered is only that which gives character to a given area. Although gradual changes in vegetation, such as often occur in passing from one area to another, give rise to more or less wide transition zones, they are not represented on the map as they are on the previously described map by Shreve. Lines separating well-characterized vegetation areas were drawn through points in the transition area determined entirely from empirical bases, as gradual changes in vegetational characteristics do not permit precise demarcation.

Zon recognizes the forests of the United States as forming two broad belts corresponding with the Atlantic and Pacific regions of Sargent and other forest geographers. These two regions are effectually separated in the central part of the continent by grassland, and embrace nearly one-half the total area of the country (48 percent). The eastern forest was originally unbroken and essentially broadleaved in character, the western much broken by intervening grassland and desert and essentially coniferous. As classified and mapped by Zon, the eastern region comprises 7 major areas of forest vegetation or natural forest subdivisions and the western 5. The nomenclature employed is derived from dominant species rather than from physiological distinctions descriptive of the character of vegetation. It also indicates geographical location of the areas. Although Zon's classification and map, like Shreve's, is based on vegetational criteria, the units conceived are not of the same degree of magnitude. Zon recognizes 12 large forest subdivisions and Shreve but 10.

The eastern region. — Owing to the less mountainous character of the eastern region, the natural forest vegetational units of large magnitude very largely coincide with geographical regions, rather than with topo-

graphic form as in the west. The line of division between contiguous units is often uncertain because of almost imperceptible transitions from one to another. However, the following 7 major natural divisions of eastern forest are recognized and described in more or less detail:

1. Spruce-fir (northern coniferous forest).
2. White pine-Norway pine-jack pine (northeastern pine forest).
3. Birch-beech-maple-hemlock (northeastern hardwood forest).
4. Oak (southern hardwood forest).
5. Cypress-tupelo gum-red gum (southern river-bottom forest).
6. Longleaf pine-loblolly pine-slash pine (southeastern pine forest).
7. Mangrove (subtropical forest).

The southern hardwood forest in the above classification was originally continuous. It has been greatly modified by cultural activities but is still clearly separable into the following 3 secondary units:

1. Chestnut-chestnut oak-yellow poplar forest.
2. Oak-hickory forest.
3. Oak-pine forest.

The western region. — Owing to the mountainous character of the western region with its abrupt topography and great climatic differences, the forest is more or less discontinuous. Five major natural divisions or large vegetational areas are recognized, of which 2 are classed as woodland and 3 as timberland. Each of these areas is delimited on the map and described. They are:

1. Chaparral (southwestern broadleaved woodland).
2. Piñon-juniper (southwestern coniferous woodland).
3. Ponderosa pine-Douglas fir (western pine forest).
4. Cedar-hemlock (northwestern coniferous forest).
5. Spruce-fir (northern coniferous forest).

The western pine forest in the above classification is more or less broken by other types of vegetation because of its rough topography. It is divided into 3 secondary natural divisions:

1. Ponderosa pine-sugar pine forest.
2. Ponderosa pine-Douglas fir forest.
3. Lodgepole pine forest.

Although the western pine forest is placed on the map in three colors corresponding to the divisions noted above, the text accompanying the map recognizes large, widely distributed pure forests of ponderosa pine, also pure forests of Douglas fir in the Rocky Mountains. It also recognizes the more or less temporary character of the lodgepole pine forests of Montana, Wyoming, and Colorado and the western larch-Douglas fir forests of northwestern Montana and northern Idaho.

The northwestern coniferous forest which is much less interrupted by other vegetational types is divided on the map into 3 secondary units:

1. Western white pine-larch forest.
2. Douglas fir forest.
3. Redwood forest.

Zon contends that, although the western white pine-larch and the Douglas fir divisions differ greatly in composition, their physiological characteristics are reasonably uniform and everywhere they tend toward the western red cedar-hemlock climax. The western white pine-larch division is confined chiefly to northern Idaho and adjacent portions of Washington and Montana. The Douglas fir division is confined chiefly to western Washington and Oregon.

Redwood, although classed in the northwestern coniferous forest (the cedar-hemlock series), and isolated communities like Monterey pine and Monterey cypress, now occupying very localized areas, are recognized as remnants of major vegetational divisions now largely extinct.

17. FOREST COMMUNITIES OF VARYING DEGREES OF MAGNITUDE

An effort has been under way for some time to obtain a general agreement regarding the classification and nomenclature of forest communities. Extensive areas such as the northwestern coniferous forest and the prairie grasslands, determined chiefly by climate, are climatic formations and areas of less magnitude such as river-bottom forest and marsh grassland, determined chiefly by physiography, are physiographic formations. The *association* has been characterized by Raunkiäer (1905, 1934) as a qualitatively and quantitatively homogeneous plant community. It is a community of plants which occupy a common habitat and is distinguished in terms of vegetation.

18. Forest Formation

Since the time of Grisebach (1838), who first used the term *formation* to represent a unit of vegetation, the term has been used in widely different senses. He calls a group of plants which bears a definite physiognomic character, such as a meadow or a forest, a phytogeographic formation. From this it appears that Grisebach's conception of formation was essentially physiognomic. Drude (1890), on the other hand, regards a plant formation as within a definite phytogeographic flora and determined by its dominant species, although its permanent composition is affected by the definite conditions of the site which keep it distinct from adjacent formations. Cowles (1901) and Moss (1907) were among the first to take development into consideration in deter-

mining plant formations. Moss states that "a plant community with patches of bare soil here and there is open and represents an early stage in succession which finally leads to a condition in which the ground is fully occupied by one or a few dominating species and ultimately to a condition of stability. The whole series of stages which began as an open or unstable vegetation, passing through the successive changes up to the stable community, is a formation." Although Moss bases the determination of plant formation primarily on site, development is assigned a definite and real significance.

Climatic factors, particularly air temperature and humidity,[1] make it possible to recognize as distinct vast regions, each dominated by a characteristic vegetation, called by Schimper (1903) a climatic formation. In contrast to the climatic formation which is extensive because the factors which produce it are widespread, is physiographic formation which is more restricted because the factors which produce it are more or less local and largely controlled by physiography of the locality. Within every climatic forest formation there are a variable number of permanent plant communities of distinct growth forms, due largely to the effects of physiographic variation on the direct site factors. Schimper used the term edaphic or local formation to designate these permanent communities whose vegetation is chiefly determined by physiographic differences. They are here recognized as physiographic formations.

19. Climatic Forest Formation

Climatic forest formation may be defined as the forest vegetation of an entire region in which, taken as a whole, climatic features are similar or uniform. It is a unit from the standpoint of climate. Owing to the existence of various broad types of climate parallel types of climatic forest formations have been developed. Thus the sclerophyllous woodland formation of southern California is paralleled by the same type of formation in the Mediterranean region and in South Africa.

Climatic forest formations which occur in different regions in response to the same type of climate may be said to belong to the same

[1] Temperature conditions and moisture conditions are usually considered separately in vegetational studies by the analytical method. They are, however, interdependent in their effect on vegetation. Thus temperature has a marked influence on both rainfall and evaporation and an area of low temperature may have a high soil moisture due to a relatively low evaporation.

climatic formation. In general, as emphasized by Nichols (1917, 1923), the ecological aspect of the climatic formation is determined by that of the climax plant communities of the region.

20. Physiographic Forest Formation

There are usually a number of physiographic formations within a given climatic type. The boundaries of these communities are controlled primarily by the topographic features of the region. These physiographic formations within a climatic type, taken collectively, are called by Nichols (1917) a physiographic formation complex, which is equivalent to the climatic formation. They are units from the standpoint of physiography. Thus in a given climatic unit there may be excessively wet and overly dry areas which bear a vegetation composed of growth forms quite unlike those of average upland. These form physiographic formations. They are differentiated by differences in growth forms due to physiographic differences in the climatic type.

21. Development of Forest Formations

The recognition of climatic and physiographic forest formations should take into account the developmental concept (Clements, 1916). A climax stage in a climatic forest formation is relatively fixed through a climatic era. No marked change in the vegetation is possible without external disturbance. The reaction of the existing vegetation is neither favorable nor unfavorable to other growth forms. In all preliminary stages, however, the particular vegetation present at any time, due to its own reactions on the site, is replaced in time by another representing a higher stage in the progress toward the climax.

The climax stage in a physiographic forest formation is fixed during a period of slight change in topographic form and climate. Cowles (1901) has emphasized the necessity for succession in physiographic formations to correspond with the order of succession of topographic forms in the landscape. As time passes, one physiographic formation is replaced by another, though by imperceptible gradations, just as topographic change is toward a base level. The uplands are worn down by wind and water erosion and swamps and lakes are gradually filled. As a region passes from youth to old age it tends, therefore, to lose its extremely wet and overly dry areas and to gain in areas having soil conditions favorable for plant growth. The tendency is away from both hydrophytism and xerophytism toward mesophytism, or toward the climax vegetation of the climatic type.

Both climatic and physiographic forest formations at any given time may include certain sites with climax vegetation and others with vegetation in various stages of succession.

22. Delimiting Forest Formations

Recognition of climatic forest formations is based upon distinctions in upland climax vegetation interpreted by the course of succession. They are coexistent with climatic types. Differences in forest vegetation would disappear were the topography within a climatic unit area brought to a base level, and all the vegetation were climax, for all the vegetation would then be a single climax community. The same type of climatic forest formation may repeat itself in more or less widely separated places because of conditions which result in a similar climate. Theoretically all vegetation of a climatic type is tending toward the degree of mesophytism which characterizes the formation as a whole because of succession and the leveling of hills and the filling in of low places. This theoretical condition, however, is never attained because the climax is never reached at the same time over all parts of a climatic unit area, for surface drainage and crustal movements (uplifts and subsidence) prevent the leveling of the surface to a base level.

Succession due to change in physiographic form on high and exposed sites is from xerophytism toward the degree of mesophytism which characterizes the climatic type as a whole. On the other hand, in the low depressions it is in the reverse order, namely, from hydrophytism toward the degree of mesophytism which characterizes the climatic unit as a whole.

The demarcation of physiographic forest formations is based on changes in growth form due primarily to changes in topography, and secondarily to changes in soil. As a climatic unit area is never reduced to a base level, varying topography causes local climatic and edaphic variations which in time cause succession to be arrested in its progress from xerophytism toward mesophytism and also in its progress from hydrophytism toward mesophytism at various stages before the highest type of mesophytism for the climatic area is attained. Vegetation represented by each of these arrested stages is the climax vegetation of its particular site until changes in topography make possible further progress in vegetation toward the highest type of mesophytism for the climatic area. Each is a physiographic climax (Nichols, 1923).

Topography as related to the physiographic history of the entire climatic area is of fundamental importance in the demarcation of physiographic forest formations. Although present-day features of the

topography of any region are a result of progressive development, for purposes of differentiating forests into natural vegetation units, topography must be regarded as stable with the exception of the few places where rapid changes are taking place. On the whole, soil appears to be secondary to topography in determining the character of vegetation although there are notable exceptions as, for example, the pine barrens of New Jersey and Long Island, New York, and the sandhills of the Carolinas. Both topography and soil must be considered in the demarcation of physiographic forest formations.

23. Forest Association

Like formation, the term *association* as applied to forest vegetation has been used with widely varying meanings. From the point of view of physiographic ecology the association is now recognized by most ecologists as the fundamental unit of vegetation. The nature of the site is the basic cause of an association. It is most readily distinguished in terms of vegetation.

Although an association is a community of plants which occupy a common habitat, all plant groups are not necessarily recognized as associations. It is only those in which the vegetation taken as a whole exhibits uniformity in ecological structure, including physiognomy and floristic composition.

Ecological structure embraces all characteristics in the vegetation which are of ecological significance. Physiognomy is the outward appearance of a community based on the nature of the larger and more common plants that enter into its composition, that is, the character and abundance of its dominant growth forms. Floristic composition relates to the species which are more or less uniformly preponderant, more particularly in relation to their mass effect. The dominants (to some extent the subdominants) typify the characteristic growth forms of the association.

By some ecologists a forest association has been considered a concrete piece of vegetation in the spatial sense, by others as the aggregate in an abstract sense of all the individual pieces of the same kind of vegetation irrespective of geographical location.

Nichols (1917) illustrates these conceptions as follows:

> We have in central Connecticut any number of pitch pine communities, all of them essentially alike in their vegetation but all, broadly speaking, topographically separated from one another and therefore organically disconnected. Now to some ecologists each one of these pitch pine communities, by itself, is an association. To others the term pitch pine association implies a sort of pigeon-

hole to which all the individual pitch pine communities can be referred; the individual community is merely a concrete example of the abstract association. Still others would say that all the individual pitch pine communities in existence, considered as a single aggregate and concrete whole, constitute the pitch pine association and that the individual pieces of vegetation themselves are but parts or fragments of this association.

From the above it appears that association in the concrete is a piece of vegetation characterized by homogeneity and uniformity in structure of vegetation and in the abstract in the constancy of this structure wherever the vegetation is found.

Although an association in its ecological aspect is essentially homogeneous throughout, floristically it exhibits more or less variation. Where variations in vegetation concern the dominant species, it is usually possible to distinguish different *consociations* characterized by Clements (1916) as subdivisions of the association with single dominants. When the variation in an association is in species of secondary importance, *societies* may be recognized. A mixed hardwood forest of southern Connecticut may be essentially uniform as to dominants, or in places a particular species like red oak may be dominant and give rise to a distinct consociation. So also the subordinate vegetation, such as shrubs and herbaceous vegetation on the forest floor, may vary locally, giving rise to distinct societies. Consociations and societies are units representing floristic variations within an association.

There is within every formation, when considered in a spatial sense, a number of climax or permanent associations and usually a larger number of temporary associations. Climax associations have attained the highest degree of mesophytism which the nature of the environment permits. Thus birch-beech-maple is a climax association in central New England; also oak-hickory is a climax association in places in southern New England. They are associations which have reached a condition of equilibrium in respect to site factors. Temporary associations, on the other hand, like gray birch, have not reached a condition of equilibrium but are destined sooner or later to be superseded by more mesophytic types of vegetation.

Where conditions for upland growth within a climatic area are most favorable the climax association for that particular climatic type is capable of attainment, but where less favorable the succession stops short of it; hence we find in every climatic unit some associations less mesophytic than the true climax association. They are, however, permanent in the sense of admitting no further succession under existing physiographic conditions and must be regarded as climax associations.

Nichols has proposed the term physiographic climax association for those associations in which succession has been arrested short of the climax association. Although they are less mesophytic, for all practical purposes they are permanent and should be regarded as climax associations. Thus the New Jersey pine barrens, although in a climatic unit capable of supporting a highly mesophytic forest, are in a subclimax stage far short of it. (See Chapter XVIII.)

24. FOREST TYPES

A discussion of ecological units of forest vegetation logically involves a consideration of forest types. Forest type as used in the classification of forest vegetation has come into forestry literature within comparatively recent years, namely, since the development of the ecological concept in the study of vegetation. It is used much more in forest descriptions and in forest mapping in this country than abroad. The reason for this is that a classification into types is more useful in virgin forests than in cultivated forests where a purely artificial division into stands is usually sufficient. Although a considerable part of recent forestry literature in this country is given to description of forest types and to maps showing their location and boundaries, the bases for typing have been widely different. As a consequence forest types as conceived by one writer are not the same as those of another. Apparently the term forest type was first used by Graves (1899) who characterized it as follows:

> If nature is left undisturbed, the same type of forest will tend to be produced on the same classes of situation and soil in a specified region. There will be variations within the type, but the characteristic features of the forest will remain constant, that is, the predominant species, density, habit of trees, reproduction, character of undergrowth, etc. If a portion of the forest is destroyed by fire, wind, or otherwise, the type may for the time being be changed; but if left undisturbed it will revert to the original form, provided the condition of the soil is not permanently changed. Thus in the Adirondacks, a group of spruce and pine on an island may be replaced after a fire by white birch and poplar. After a time, however, the former will creep back, and grow under the thin cover of birch and poplar, and eventually crowd them out. A good illustration of the same principle is found in Massachusetts, where in many sections the white pine formed an important feature in the original forest. After the pine was cut off, the hardwood predominated in the second growth. Now, however, there is abundant evidence that the white pine is increasing in quantity, and if the woods were left untouched the original type would return.

The principles upon which forest types should be based have been stated by Zon (1906) as follows:

> A problem most peculiar to our forest conditions and promising, if properly

solved, most productive results is the problem of forest types. . . . There can be no real progress in our silvical studies until the question of forest types is solved. . . . It [ecology] describes the existing plant societies, as far as they can be divided into distinct groups with well-defined features, and endeavors to find the reasons that caused them to group together and the factors that made them assume their characteristic features; in other words, just what silviculturists have been trying to learn for over a century regarding tree societies. . . . The physical conditions of the situation, then, are the main factors which determine the whole character of the forest type. . . . In this classification the differences in the character of forest growth must always be considered since only by going back and forth from the physical conditions of situation to the character of forest growth can the relationship between the two be determined. . . . Having accepted the physical conditions of the situation as the basis for dividing a forest into types, we must find some criterion to guide us in deciding what differences in the physical conditions justify the establishment of different types. Such a criterion is in the reproduction of the forest. . . . Only such differences in the physical conditions as are followed by differences in reproduction justify the segregation of stands into separate types. . . . One of the most important characteristics of a forest type is its stability. . . . The study of the habits of our forest trees must be confined to definite forest types; we have no right to speak about the silvical features of spruce, white oak, or any other species in general, but only as members of definite forest types.

Clements (1909) emphasizes the desirability of harmonizing forest types with ecological units. He says:

The application of forest types to forestry brings them into harmony with the fundamental principles of ecology. It places the forester and ecologist upon the same basis insofar as the study of forest vegetation is concerned. . . . Detailed knowledge of a forest's development is the only scientific foundation for its treatment, but such knowledge is possible only through an investigation based upon factors, development, and structure.

Cajander (1909, 1913, 1926, 1930) and Ilvessalo (1929) have accepted the ecological concept of forest types. In interpreting the site in terms of vegetation, they have employed indicator plants as a basis for classification. The forests of Europe are, to a large extent, cultural. Dominant vegetation can not be used in typing on an ecological basis, because in many instances it has been established or modified by man and may or may not represent a full expression of the site factors. In this country, however, where most of our forests are the result of spontaneous action of nature, dominant indigenous tree vegetation is usually employed in the demarcation of forest types.

25. Concepts of Forest Types

Although in the earliest use of the term forest type, it clearly had an ecological significance, to some extent it has lost its earlier meaning and

today is used with widely differing significance by practicing foresters. This situation has arisen because of imperfect knowledge of the physical and biological factors of site and the effect of site on the development and character of vegetation and also because of the relative economic importance of different species in the recognized type.

It was natural that, with very imperfect knowledge of both site factors and vegetation and the interrelation between them, diverse ideas as to forest types and the particular factors that should be employed in delimiting them should develop. It has, therefore, gradually become the practice to divide forests into units based entirely on the species (often economic species only) that chance to be on the area at the time and call them cover types; to divide forests into units based upon one or more physical factors and call them physical types; or to divide forests on other bases and call the units temporary, management, or permanent types as the case may be.

There are many ways in which a forest can be divided into units. The division may be purely an artificial one, much the same as the farmer divides his farm into fields. The units first recognized were artificial and without conscious relation to site factors. In the evolution of managed forests and as knowledge increased regarding the effect of temperature, soil moisture, and other site factors on the character and growth of forests, it was recognized that artificial units were inadequate. Entirely for economic and practical reasons, the artificial units began to assume the character of natural units. Today foresters are searching for a means by which the forest divisions which were purely artificial and which arose from economic necessity, but are becoming more natural with the passage of time, can be fitted into the natural units of forest vegetation, as recognized by plant ecologists. Foresters have divided woodland into units on the basis of actual vegetation existing on the site, on productive capacity of the site, on volume of wood in cubic or board feet, on age, on rotation, on kind of forest to be produced, and on many other bases as well. The division of the forest into any one of the above kinds of units may be useful. For certain purposes of administration and economic utilization one may be necessary at one time and another at some other time. The real economic need for classifying forest vegetation into different kinds of units has given rise to so-called types derived from different bases. The kind and degree of difference necessary for the demarcation of forest types are unsettled at the present time. There has, however, come into general use the following type names, according to the basis adopted for classification: cover type, temporary type, permanent type, physical

type, management type, and indicator type. All of these have been called forest types.

Although there appears to be wide divergence in opinion as to what constitutes a forest type, Clements (1920) has stated that the classification of forests into associations by ecologists and into forest types by foresters differs more in emphasis than in fact. Thus in typing a forest most foresters use the forest community as an indicator of site conditions. Even those who place first importance on physical site factors recognize the necessity for knowing the vegetation. Physical types are based on uniformity in climate and soil, which uniformity is recognized in the response made by vegetation. Although emphasis is variously placed, practically all foresters regard both site and forest community as essential to an understanding of forest types.

As the needs for forest classification have been largely in connection with forest description and in the differentiation of cover according to species, the term cover type has given way to the term forest type and is so used by most foresters. Management types and those derived from other bases are as much forest types as are cover types.

26. **Cover Type.** — The cover type is based on composition of the forest, relative percentage of important species, their relative economic importance, and their differences in volume. It only considers the vegetation present at the time being, without in the remotest way relating it to site factors or environment. It conveys no conception as to whether the type is temporary or permanent or whether it will be successful under forest management. It is the simplest classification that can be applied to forest vegetation.

27. **Permanent Type.** — A permanent type is also called the climax type. It represents the most mesophytic vegetation capable of natural development on the particular site. It is the vegetation that will ultimately take possession of and perpetuate itself on any given area when natural conditions are undisturbed.

28. **Temporary Type.** — In a temporary type the vegetation is recognized as a stage in the development of a forest toward the climax vegetation for the particular site. It results from interference with natural conditions of the site because of clearing, fire, or lumbering. Its natural tendency is to develop from one temporary type through another to the permanent or climax type.

29. **Physical Type.** — A physical type is a unit based on forest-producing power as determined by the physical factors of site. The unit is based on land, not on vegetation. In its practical application

in mapping forest vegetation the vegetation present on the site is usually accepted as an indicator of site conditions. Although vegetation of the permanent type is an excellent indicator of the physical type, vegetation in stages of succession below the permanent or climax type is not.

30. **Management Type.** — A management type is the kind of forest vegetation that foresters aim to obtain through conscious silvicultural management. Although sometimes it is coincident with the temporary type and at other times with the permanent type, its floristic characteristics and manner of development are consciously shaped for economic ends.

31. **Indicator Type.** — An indicator type is a unit of vegetation based primarily on the same quality of site as indicated by one or more " indicator " plants, characteristic of the unit area as a whole.

32. Relation of Forest Types to Ecological Units

Although various kinds of typing are useful in forestry, the goal of silvicultural research is to establish the relation between forest vegetation and its environment. Any division of a forest into units which does not take into account both vegetation and environment is more or less artificial. Although it may be useful for management and descriptive purposes, it can not help in determining the fundamental causes of different natural units of vegetation, nor make it possible to understand the development of vegetation and the physical and biotic factors by which it is controlled. The development of silviculture rests upon a thorough understanding of the interrelations between forest vegetation and site. It is only by correlating vegetation and site and considering site as the cause and a forest as the effect that silviculture can be placed upon a natural and safe foundation. So long as the units of forest vegetation into which foresters divide forests are correlated with differences in the combined site factors, we know that the division is natural.

In any given region, owing to an existence of parallel series of habitats, parallel series of associations have been developed. If habitats forming a given series are equivalent to one another, they may be referred to as a common habitat type. Associations that are correlated with habitats which form a habitat type agree with one another in ecological aspect, although they may differ in floristic composition (Nichols, 1917). In general, it is possible to group the many associations in a given plant formation into a comparatively small number of

association types. As with associations, association types are named in terms of vegetation. Thus, the oak-hickory association type of southern New England includes such associations as the red oak-hickory association, the chestnut oak-hickory association, and the black oak-hickory association. Forest types, like the forest association types, are correlated with a common habitat type. Although habitats forming the habitat type are similar and the vegetation has the same ecological aspect, the floristic composition of one member of the series differs from that of another in the degree of dominance of component elements. Because of these differences, one may recognize a variable number of subtypes within the ecological forest type. These subtypes correspond to associations and consociations.

In typing a given forest from an ecological point of view, any particular piece of vegetation within a formation and considered in a spatial sense that differs in ecological structure is an organic unit, namely an ecological forest type. Pieces of vegetation within a forest type which differ from each other in floristic composition, particularly with reference to dominance are ecological forest subtypes. They are forest types and forest subtypes in the concrete. All pieces of like vegetation, without reference to location, comprise types and subtypes in the abstract.

A permanent forest type is the equivalent of a climax forest association type and represents the highest degree of mesophytism that a forest is capable of attaining on its particular site without climatic or physiographic changes. Temporary forest type is the equivalent of temporary forest association. It has not reached the stage of equilibrium characteristic of a climax and is merely a transitional stage in a successional series. Cover type, as at present recognized and based on floristics and economics, has no equivalent in ecology. It takes no account of site factors, consequently temporary and permanent forest communities with unlike site factors may fall into the same cover types so long as the dominant species are the same. Physical forest type has no equivalent in ecology as it is based on physical factors of the site and entirely ignores the resulting vegetation. It may be applied to sites without forest vegetation. Management type is a permanent or climax forest association when coincident with a permanent forest type. It is a temporary forest association when coincident with a temporary forest type. It is usually a temporary association because it persists only so long as it is given conscious care. It is usually a more or less artificial stage in a succession series, which, if left undisturbed, ultimately attains the climax for the particular site.

33. Usefulness of Type Concepts

Much confusion has resulted from the typing of forest vegetation with emphasis placed in the direction most useful for a particular purpose. Thus a classification which recognizes 6 forest types in the eastern spruce region, namely, swamp, spruce flat, hardwood, spruce slope, birch and poplar, and old field is a mixed classification named partly from floristics, partly from site, and partly from floristics and site combined. A clear conception of forest types makes it imperative that those derived from different bases be kept distinct. In typing, it is impossible to combine cover types, physical types, and other kinds of types in the same series.

34. Application of Cover Types.—The division of forest vegetation into units based on cover, considered from an economic as well as from a floristic standpoint, is practically useless in purely silvical investigations. The classification of forests, however, into these units is of utmost importance in the reconnaissance of extensive areas where the primary objects are to obtain an inventory of the timber, determine the principal species, and judge their quality and value. Such a classification usually precedes all others in the organization of wild land for forest management.

A standard system of classification of cover types has been adopted by the U. S. Forest Service for use in the national forests (1925). The basic features of this classification are:

1. The names of units are usually taken from the most distinctive commercial species, whether or not they form the largest percentage of the stand.
2. No attempt is made to provide for all possible combinations of species. The aim is to keep the classification practical; consequently only such units as occupy sufficient area to be of importance in forest management are included.
3. The percentages given in type descriptions are percentages of the numerical proportion of trees 8 inches and over in diameter, or of trees which form the main stand and those which it is reasonable to suppose will eventually come up into the main stand.

In this classification, which is entirely for practical purposes, all cover types are placed under 3 general headings, namely, treeless types, woodland types, and timberland types. The former includes not only barren areas, cultivated areas, and grassland, like alpine meadows and parks, but also brush, sagebrush, and chaparral. Woodland includes tree-covered areas usually at the lower altitudinal limits of tree growth in semi-arid regions, where the vegetation in its climax form occurs in open stands of low, crooked individuals. The timberland types include all areas on which trees when mature are in closed stands. The

individual trees are tall, straight, with considerable clear length and are useful for sawlogs and for similar purposes.

35. Examples of Regional Classification of Cover Types. — The following classification of cover types employed in the Central Rocky Mountain Region (Region 2) is typical of the U. S. Forest Service method of describing cover types for the western United States in which 34 cover types have been recognized (U. S. Forest Service, 1925). Three general classes of vegetation are recognized, namely (I) Treeless; (II) Woodland; (III) Timberland. Each of these is divided into types as follows:

I. Treeless areas (types in)

1. Grass. Both above and below the altitudinal limits of tree growth and to some extent interspersed with tree growth. Park or mountain meadow whose principal vegetation is grass and other herbs.
2. Barren. Rocky, exposed, or arid areas at high elevations, and other areas which do not support trees or grass or more than a very scattered growth of herbs or shrubs.
3. Cultivated. Areas now under cultivation or lying fallow.
4. Sagebrush. Areas where the principal vegetation is sagebrush.
5. Brush. Areas where the present cover is shrubs or stunted trees, excepting oak.

II. Woodland areas (types in)

Usually at the lower altitudinal limits of tree growth. The crop when mature is chiefly useful for cordwood, fencing, etc.

6. Piñon-juniper. Areas where 80 percent or more of the stand is piñon and juniper in varying proportions. Piñon, one-seeded juniper, and Rocky Mountain red cedar are the chief species often with some of the Rocky Mountain white oaks and ponderosa pine.
7. Juniper. Areas where 80 percent or more of the stand is any species of juniper with little or no piñon. Rocky Mountain red cedar is the chief species usually with some limber pine, ponderosa pine, or Douglas fir.
8. Oak. Areas where approximately 60 percent or more of the stand is one or more species of western oaks. Gambel oak is the chief species and is usually quite scrubby.

III. Timberland areas (types in)

Areas where the crop, when mature, is a more or less dense stand of trees useful for sawlogs, ties, and telegraph poles.

9. Ponderosa pine. Areas where approximately 50 percent or more of the stand is ponderosa pine. Usually on dry, well-drained sites at the lower altitudinal limit of timberland or on exposed south and southwest slopes at higher elevations. The principal species in mixture are Douglas fir, white fir, blue spruce, and lodgepole pine.
10. Lodgepole pine. Areas where approximately 50 percent or more of the stand is lodgepole pine. Usually nearly pure, but sometimes in mixture with other species. The principal species in mixture are Douglas fir, Engelmann spruce, alpine fir, blue spruce, bristlecone pine, and limber pine.

11. Bristlecone pine. Areas where approximately 60 percent or more of the stand is bristlecone pine, often in mixture with limber pine, lodgepole pine, Engelmann spruce, blue spruce, Douglas fir, and white fir.
12. Limber pine. Areas where approximately 60 percent or more of the stand is limber pine, usually in mixture with lodgepole pine, Douglas fir, Engelmann spruce, and alpine fir. Seldom in pure stands.
13. Douglas fir. Areas where 60 percent or more of the stand is Douglas fir. Principal species in mixture are ponderosa pine, lodgepole pine, limber pine, white fir, and blue spruce. This type is often preceded by a temporary type of aspen.
14. Engelmann spruce. Areas where 50 percent or more of the stand is Engelmann spruce. This type sometimes follows a temporary type of aspen. It may occur as a pure type, but more often as an admixture of alpine fir, lodgepole pine, or Douglas fir, and occasionally bristlecone pine. It is usually at the higher elevations on moist sites.
15. Subalpine. Areas which support a varying mixture of subalpine species, no one of which is abundant enough to classify the stand in one of the types already described. This type is at the upper limits of tree growth and is usually unmerchantable because of the poor form and small size of the trees. The principal species are alpine fir, Engelmann spruce, lodgepole pine, limber pine, and bristlecone pine.
16. Aspen. Areas where 60 percent or more of the stand is aspen. This type is usually nearly pure, but also occurs with various conifers in mixture at medium to high elevations. It is usually on fairly moist sites. Where no market for aspen is available, these areas are sometimes mapped as young age classes of a conifer understory often present.

A somewhat similar system of forest cover types for the United States east of the Great Plains has been prepared by the Committee on Forest Types, Society of American Foresters (1940). In this classification 97 types are described, 26 in the northern forest, 35 in the central forest, and 36 in the southern forest. The committee responsible for this classification accepted the usual definition of a *cover type* as being a forest type now occupying an area without implication as to whether it is temporary or permanent, but with the reservation that present composition of a stand rather than its later development should be the primary basis for recognition of forest types. However, forest cover types of a temporary character as well as those of a climax nature are dependent upon the climatic, edaphic, and biotic factors of site. Although the ecological relationships of forests, especially forest succession, must be recognized in forest management the committee, in selecting the combination of species to be recognized as forest types, adhered to the following principles:

1. A cover type must actually be found occupying in the aggregate hundreds of thousands of acres. This does not require that the type cover any single large area in a solid stand, but rather that it be of a characteristic composition found here and there throughout a considerable range of country.

2. A cover type must be distinctive and easily separated from other cover types which most closely resemble it.

3. Within the foregoing limitations every important combination of cover must be recognized as a forest type.

Each type recognized by the committee of the Society of American Foresters is described but is not so rigidly defined as are the forest types described by the U. S. Forest Service for the western United States. The types were named, so far as practicable, after one or two, or at most three, predominant species. This list of types is so arranged as to permit and to encourage either expansion or contraction in the number of types recognized by any person, depending upon the purposes and circumstances of use. Further study may also suggest necessary modifications. Representative types under this classification are described as follows:

TYPE 9 WHITE PINE

Composition: White pine pure or predominant. Pure stands of white pine are characteristic. Associates: In the North on light soils Norway pine, pitch pine, gray birch, aspen, red maple, pin cherry, and white oak. On heavier soils paper birch, black birch, yellow birch, gray birch, black cherry, white ash, red oak, sugar maple, basswood, hemlock, and red spruce. In the Southern Appalachians on moist sites yellow poplar, chestnut, hemlock, red oak, and white oak. On drier sites chestnut oak, scarlet oak, shortleaf pine, and pitch pine.

Occurrence: Most commonly within southern and lower portions of the northern forest from southwestern Maine to east central Minnesota and along Appalachian Mountains to northern Georgia. Most abundant in central New England and in the Lake George and Lake Champlain section of New York at elevations from sea level to 2,500. In the Southern Appalachians of West Virginia, Virginia, Tennessee, North Carolina, and north Georgia, generally at elevations of from 1,500 to 4,000 feet, but occasionally as high as 4,700 feet. Formerly best developed in Tennessee and North Carolina between 3,000 and 4,000 feet. In the Lake States chiefly in central part of Michigan and in north central Wisconsin and in north and east central Minnesota; less common northward. Elevations from 700 to 1,700 feet. Typical on fresh, sandy loam upland but occurring occasionally on clay, in swampy areas, and on loamy sands. In the Northeast occurs on abandoned agricultural land of all soil types. In the Southern Appalachians on mountain slopes, flats, and valleys varying widely in soil character from sandy to clayey loam and from relatively moist to dry. Extensive areas occupied in the Northeast, elsewhere in small stands widely scattered.

Place in succession: Frequently first type to occupy agricultural land after abandonment. Approaches permanence on sandy soils. On heavier soils usually succeeded by sugar maple-beech-yellow birch, red oak-basswood-white ash, white pine-red oak-white ash, white pine-hemlock, sugar maple-basswood, white oak or white spruce-balsam fir-paper birch. A long-lived temporary type seldom succeeding itself except after fires or under special cultural treatment.

Importance: Important commercial type in New England and Essex, Warren,

and Saratoga counties, New York; about 100,000 acres scattered through Pennsylvania. Elsewhere because of relatively small area covered, not of primary importance.

Variants and synonyms: White pine-Norway pine. Bergman and Stallard, *Minn. Bot. Studies* 4, part 4 (1916), 333–378; Buhler, *Minn. State Forester, 3rd Ann. Rpt.* (1913), 120–135; Roth, *U. S. F. S. Bul.* 16 (1898). Pine-spruce, Stallard, *Ecology* 10 (1929), 476–547. White pine-balsam-hemlock. Whitford, *Bot. Gaz.* 31 (1901), 289.

Type 53 Yellow Poplar

Composition: Yellow poplar pure. Associates: black locust, red maple, black birch, red oak, cucumber magnolia, and other moist site species.

Occurrence: Appalachian Mountains and adjoining portions of the central forest, at altitudes of 500 feet (or less in the north and west) to 4,000 feet in the southern Appalachian Mountains. On moist lower slopes, northerly slopes, moist coves, and flats. Usually in small scattered stands. Frequently in more or less interrupted strips at bottoms and sides of mountain coves.

Place in succession: Characteristically a second-growth and temporary type often found in old fields. In small patches yellow poplar still predominates in old-growth stands, and the yellow poplar type may once have been extensive in the virgin forest. In its pure form the yellow poplar type is not a climax. Stoneburner, for the Unaka National Forest, reports the yellow poplar type as rapidly replacing white pine-hemlock stands after logging.

Importance: Extremely important in the Appalachians both commercially and in aggregate area. Relatively accessible due to its occurrence in coves and on lower slopes.

Type 73 Longleaf Pine-Slash Pine

Composition: Longleaf pine and slash pine alone or with a small mixture of water oak and laurel oak and occasionally post oak, blackjack oak, and live oak. On ground intermittently wet loblolly pine, sand pine, southern cypress, pond cypress, black gum, and tupelo gum are characteristic associates.

Occurrence: Coastal Plain from Georgia to Louisiana. Usually second-growth stands coming in on longleaf pine ridges in the flatwoods or in old fields. Also on borders of ponds on ground intermittently wet.

Place in succession: Temporary type caused by hogs tending to eliminate longleaf pine or by fire protection favoring slash pine. Probably succeeded by longleaf pine type.

Importance: Important timber type.

Variants and synonyms: Flatwoods pine. Palmetto flatwoods. Harper, *4th Ann. Rpt., Fla. Geol. Survey* (1911) 66. Pine barrens. Hoke, *Naturalist's Guide to the Americas* (1926) 455. Pine barren flats, Harper, *Naturalist's Guide to the Americas* (1926) 116. Pine meadows, Harper, *4th Ann. Rpt., Fla. Geol. Survey* (1911) 72.

More recently (1945) a similar classification and description of the forest cover types of western North America has been prepared by another committee of the Society of American Foresters on essentially

the same basis as that used for the cover types of the eastern United States.

36. Application of Management Types. — The management type, being the form of forest cover that foresters desire to obtain through silvicultural management, is seldom the type that would naturally result from the full expression of the site factors. Very often the crop which it is best for foresters to produce from an economic standpoint is one which is not in equilibrium with the site factors. It can only be produced on a given site by scientific management. It would disappear in time were it left to compete with the indigenous vegetation. The natural cover types of southern New England are mixed hardwoods. For purely economic reasons some of these are in the process of changing into management types of white pine and red pine. Pine, however, is not at all the type of vegetation that would be produced naturally by the full expression of the site factors. Because of the higher value of the timber it pays better to grow it than to continue the natural type of the region. Greeley (1913) states:

There have been three general stages in the work of the Forest Service, each involving a somewhat different point of view in the classification of forest types. The first was during the period when the national forests were being selected and their boundaries defined. In that work we were concerned altogether with forest cover as distinct from other kinds of cover, and went no farther than the amount and composition of the stands which were actually found on the ground. The second stage is the administration, in which we are interested, in timberlands primarily from the standpoint of what they are producing and what they can be made to produce under scientific treatment. The study and classification of forests is for the purpose of management, however specifically it may be expressed. We are now entering a third stage, which will be coincident in time with the second, but which I have designated separately because of the new problems and points of view which it involves. This is the development in our work marked by intensive studies of physical factors, soil, climate, water, topography, and the rest, for the purpose of classifying lands or in connection with the determination of yield and intensive silvical research. It is the stage, or rather phase, of our work in which the physical conditions making up the site become of primary importance in the study of forest lands.

During the first stage of the work of the Forest Service the cover type in its simplest terms was adequate. In its second stage the cover type in itself is inadequate. We need rather the management type. In the third phase of work we need possibly an additional type, namely, the physical type or land type.

The management type, in my judgment, is the key to the classification of complex stands arising from changes in composition at different periods in the life history of the forest. In the stands of northern Idaho, where larch follows forest fires, white pine follows larch, and hemlock and other tolerant species follow white pine, with every conceivable gradation and mixture growing out of this rotation, I believe that our classification can be made clear and simple by

selecting white pine as our management type, the species which, first and last, is the best index of the type in all of its changing compositions, and which unquestionably we will utilize chiefly in management. In such stands I would classify all of the varying compositions as the white pine type.

37. Application of Physical Types. — As physical type refers to an area considered with reference to its forest producing power as determined by the physical factors of a site, it is the land and not the forest which is emphasized in the classification.

Munger (1913) defines physical forest type as an area of woodland over which the physical conditions of climate and soil are so similar that a uniform method of silvicultural management may be applied to it. As many types are distinguished as variability in the physical factors and intensity of management require. The degree of difference in site factors necessary to result in another type is not fixed; the division can be made on as broad lines or on as narrow lines as seems best to fit the forest description and management. Under this conception but 9 types are recognized over the entire forested area of Washington and Oregon, namely, bottomland, lower slope, upper slope, and alpine in the forests extending from the coast to the eastern foothills of the Cascades; and transition, north slope, slope, bench, and lowland types over the remainder of the region. These physical types, as indicated by their names, are determined by topography and elevation which roughly indicate climate and soil. Under this method of typing, the vegetation is not considered in making types. Areas with heavy stands of timber fall in the same type with denuded areas and grass-covered areas in secondary succession when they are controlled by a similar physical environment. This system of typing is useful in indicating quality classes or capacity of soil for production of timber. It is also useful in the location of land of agricultural value in woodland and timberland areas and in its division into units in accordance with the silvicultural treatment most acceptable for each. Under this method, the typing is along broad lines, and few types are recognized over extensive areas. The chief objections are that no attempt is made to correlate vegetation with site, and that cover is not used to assist in the interpretation of physical factors.

Like Munger, a large number of American foresters recognize forest types as divisions of forest vegetation based upon differences in physical factors alone. Woodward (1913) has shown that it is necessary, in the valuation of land for forestry purposes, to use a method of classification (typing) that will divide the different kinds of land according to their productive capacity which is dependent upon cli-

matic and soil factors. These in turn, if left to themselves, will produce a stand of relatively fixed composition which is chiefly the result of the interaction of climatic and soil factors. In fact a forest type is commonly understood to be an area in which climatic and soil factors are uniform, and which may, therefore, produce stands of like composition.

38. Application of Temporary and Permanent Types. — In the early attempts at typing woodland vegetation it was observed that not all the forest on all parts of a given area having uniform site conditions was the same. Thus in New England patches of birch and aspen were found interspersed through areas covered with spruce and pine. Here the birch and aspen have come in as a result of some interference with natural conditions, such as fire, lumbering, and insect infestations, and in time they will be replaced by other species. The temporary type is a stage in succession. A temporary birch type occurring today may be replaced later on by a permanent spruce or pine type.

The recognition of temporary forest type as the developmental or temporary association of modern ecological literature and permanent forest type as the climax association makes possible the typing of woodland on an ecological basis. Also the recognition of permanent types and their relation to temporary types in various stages of succession is essential in the natural classification of forests. The character of the permanent type is an index of site quality, for the vegetation is in equilibrium with the site factors. The character of the temporary type is not an index of site quality because the vegetation is not fully adjusted to the site. Succession is in active operation.

The classification of forests into natural units based on development is essential for a clear understanding of the natural history of forests. The division of forests into ecological units is of the utmost importance in land classification since forest cover, when interpreted in the light of site factors which produced it, is an indicator of the productive capacity of land for both agricultural and forest crops.

39. Application of Indicator Types. — There has recently come into use in Europe a method of classification of forest types, based on site as interpreted by indicator plants forming a part of the vegetation on the forest floor. The trees themselves play no rôle in this classification. This method of forest typing was developed by Cajander (**1909, 1913, 1926, 1930**) and his associates and has been extensively employed in northern Europe, particularly in Finland. Cajander bases his theory of forest types on site quality as interpreted by indicator plants. He states that there are, in principle, two kinds of forest classification, namely, a classification of stands according to quality, and a classifica-

tion of localities (sites) according to quality. The former is a classification into stand quality classes and the latter is a classification into site quality classes. Cajander stresses the point that any classification of stands into quality classes is based on yield of stands. Yield, however, varies greatly on similar sites, depending on the density, method of treatment, and species. On the other hand, the classification of sites into quality classes is an attempt to combine in the same class all areas having the same or approximately the same capacity for growing timber, irrespective of actual present yield.

Quality classes based on site are usually gauged by the yield of stands of normal quality class. For instance, the existing stand may happen to coincide with the normal quality class, but usually it does not. Actual quality is usually but a fraction of normal quality.

Cajander places great emphasis on the importance of determining site quality classes in systematic forestry. He states that it is necessary, preliminary to calculations of yield, determination of species economically most profitable, length of rotation, method of treatment most advantageous, and other matters of decided importance in forest management. He also states that the exact determination of site quality classes is indispensable in scientific research in forestry, whether based on experimentation or comparative observations. The actual quality of stands is so much a result of arbitrary operations by forest owners and a complex of factors whose effects can not be estimated in advance that its determination is scarcely amenable to scientific treatment. On the other hand, site quality is a concept the scientific elucidation of which is possible. Cajander points out that the earlier classification of sites according to quality was based on the fact that sites differ widely in respect to yield capacity. It was believed, however, that man by his operations in practical forestry exerted but a limited influence on the basic characteristics of sites; consequently an arbitrary series of site classes was established varying from the most productive to the least productive. Thus Cotta (1804) recommended a series of 100 site quality classes varying from land incapable of growing timber to land of highest productivity. As these quality classes were determined subjectively, it was impossible to differentiate among them. There was no scientific basis for their classification. Even later, when Judeich reduced the number to 5, each with two grades, the difficulty in differentiation was not overcome (Judeich and Neumeister, 1923). Need was felt for a more exact method. Although a classification based on yield taken from sample plots, bearing stands of normal quality, and the actual yield of felled stands may give reliable data, the results are seldom wholly dependable because of variations in method of estimating

by different men and divergencies in estimates obtained by different estimators.

Efforts have been made by Cajander and his associates to discover easily recognizable indicators of site quality classes, by means of which site qualities can be identified and recognized as forest types on the ground. They recognized that wherever competition for space arises among plants, plant associations occur, each more or less clearly marked off from other associations. The association in one form or another was made use of in the classification of site quality classes. Cajander's theory of forest types is really based on the classification of forest soils, indicator plants employed in the classification being indices of soil qualities. He has developed a system of site quality classes essentially independent of tree vegetation. Forest types are named from plant species which indicate the site quality classes.

Thus for Finland, Cajander (1926) recognizes a number of forest classes, such as (*a*) the dry moss (and lichen), (*b*) the moist moss, (*c*) the grass-herb, and (*d*) the spruce and broadleaf peat-moor. Each of these is represented by a number of forest types. Each type has one or more characteristic plants which indicate the site quality class and give name to the forest type. Among the forest types in class (*a*) are the *Cladina* type, the *Myrtillus-Cladina* type, the *Calluna* type, the *Empetrum-Myrtillus* type, and the *Vaccinium* type. Among those in class (*b*) are the *Hylocomium-Myrtillus* type, the *Myrtillus* type, the *Oxalis-Myrtillus* type and the *Pyrola* type. Among those in class (*c*) are the *Geranium-Dropteris* type, the *Oxalis-Majanthemum* type, the fern type, the *Sanicula* type, the *Aconitum* type, the *Lychnis diurna* type, and the *Vaccinium-Rubus* type.

Following closely Cajander's method, Ilvessalo (1929) worked out a system of forest (site) types for Canada and the northern United States. He groups the types as follows: (*a*) dry sites, (*b*) moist sites, and (*c*) grass-herb sites. The dry-site types (group *a*) are the *Arctostaphylos, Vaccinium scoparium, Calamagrostis-Arctostaphylos, Calamagrostis-Vaccinium scoparium* types; those of the moist sites (group *b*) are the *Hylocomium-Ledum, Vaccinium-Gaultheria, Pachystima, Oxalis-Hylocomium* types; and the grass-herb types (group *c*) are the *Tiarella* and fern types.

Although it appears from the work already done by Cajander, Ilvassalo, Heimburger (1934), Sisam (1938), and others that the recognition of forest types and their classification from indicator plants on the forest floor have certain advantages, difficulties are often encountered in practical application because of the frequent absence of indicator plants on sites where, under undisturbed conditions, they

would be present, and the frequency with which the investigator must resort to explaining their absence as a result of past treatment and other external disturbances, temporarily upsetting the normal course of succession (Korstian, 1917, 1919).

Unquestionably there are great advantages in a classification into forest types based on producing power of the land, irrespective of the timber thereon, as recently shown in Ilvessalo's (1926) studies. He shows that these types may serve as quality classes in the preparation of yield tables. He concludes that, since growth in all its aspects is different for the different forest types and for the same forest type differs between comparatively narrow limits, the forest types being uniform, natural, and relatively easily distinguishable, quality classes are well suited to serve as a basis for the classification of forest soils, for forest mensuration in general, and for yield tables in particular.

Studies by Tamm (1920) in Sweden reveal that these different forest types markedly influence the leaching process in the soil to different degrees, owing to quality of the humus layer that they produce.

40. Delimiting Types

The classification of forest vegetation into cover types and the mapping of them depend for accuracy upon the recognition of frequency and abundance of dominant economic species. It is purely a matter of observation, based on floristics. The mapping is relatively easy but has no permanent value. Frequency and abundance of the various species are determined by means of sample plots (quadrats) and strip surveys (transects). Sample plots are laid out in areas that are considered representative of different variations in forest cover and are analyzed and fully described. Strip surveys are run in such a manner that they cover all variations in vegetation, and differences are noted on the surveys. If sample plots and strip surveys are adequate, the types can be placed on maps from the data obtained from them. Most frequently, however, cover types are mapped in the field entirely from apparent differences in vegetation derived from observation.

The demarcation of natural or ecological types, based as they are on site factors interpreted in terms of vegetation, can not be mapped in the field without previous study. The vegetation must be examined from the basis of growth forms and from the point of view of development as well. For the most part development is determined by inference, that is, by piecing together the course of development from the various stages of succession found in the region. The demarcation and mapping of these types are impossible without experience and a knowledge of the correlation between vegetation and environment.

CHAPTER XVIII

ORIGIN AND DEVELOPMENT OF FOREST COMMUNITIES: FOREST SUCCESSION

1. CONCEPT OF SUCCESSION[1]

Forest communities (natural units of forest vegetation) arise, develop, and mature under the influence of the site factors and the reaction of vegetation upon them. The entire process of community development is expressed in forest succession. The most striking characteristic of succession is the progressive development of vegetation on the same site resulting from the successive replacement of one community by another of different growth form. Succession starts on bare areas, either areas originally bare or those that have been made bare by denudation, and progresses from one stage to another until it finally terminates in the highest type of vegetation possible under the given climatic and physiographic conditions.

Whenever the various elements in the vegetation so react upon each other and on the site that the character of vegetation as to growth form changes, through the disappearance of certain species and the invasion of others, the vegetation moves forward from one stage to another in the succession. Succession is universal in forest community development. The various stages may occur over and over again in the development of every climax forest.

No large area of vegetation is ever in complete equilibrium with the site, even in its most stable form. It is never free from smaller disturbed areas in which the vegetation is moving from one stage to another with more or less rapidity. The evidences of the successive stages in succession are most clearly emphasized on active topographic areas like sand dunes, strands, and floodplains. The development of a plant community from the appearance of the first individuals through the various stages up to the final, stabilized, or climax stage is a succession series or unit of succession. It may occur again and again on the same site in the course of time. This is illustrated where forest fires cause complete denudation. Thus a red spruce forest in New

[1] More complete treatments of the theory of forest succession are those of Clements (1909, 1916, 1928), Weaver and Clements (1938), and Phillips (1934, 1935).

England when destroyed by fire, in moving forward to the climax stage, may pass through stages characterized by the following communities:

1. Moss meadow.
2. Aster-fireweed meadow.
3. Hairgrass-sedge meadow.
4. Willow-birch thicket.
5. Aspen forest.
6. Spruce forest.

2. PRIMARY AND SECONDARY SERIES IN SUCCESSION

A primary series in succession begins with the first appearance of pioneer plants on a given site and ends with stabilization. It usually proceeds very slowly and, depending on the site, exhibits few or many stages. A vegetation which has attained its climax form or has proceeded some distance toward stabilization may be destroyed and the site made bare through some external disturbance such as fire. Denuded soils once covered with timber, if not excessively eroded, offer optimum conditions for new vegetation and the stages in succession are few and proceed rapidly. This is a secondary series and is of great importance in forestry. Secondary succession arises on areas which formerly bore vegetation but have been denuded by one cause or another. For the most part denudation owes its origin to floods, fire, animals, and the activities of man.

When denudation causes the destruction of a forest without essentially changing the soil conditions, as sometimes in forest fires, the series initiated reaches the climax in a relatively short time. When the soil is more or less seriously disturbed, as when several fires occur at relatively short intervals and erosion takes place, the conditions approach those of the original extreme and the resulting series consists of many stages which cover a long period and are far more complex. Although the causes of denudation leading to the initiation of a secondary series are many, fires, grazing, and lumbering are the most important from the standpoint of forestry.

3. Secondary Succession Following Denudation by Burning

Fires are of least significance in open communities and greatest in closed communities where they often cause complete denudation, as crown fires in the conifer forests of Washington and Oregon. Following complete denudation, the new vegetation is first composed of invaders from the adjacent unburned areas, from root sprouts, or from seed buried in the soil which escaped destruction. The rapidity with

which invaders gain entrance is dependent on their facilities for migration and their adaptability for establishment.

4. Secondary Succession Following Denudation by Lumbering

Lumbering seldom results in complete denudation. Usually only those trees are removed that can be marketed; consequently the undisturbed trees may soon take full possession of the site and the vegetation proceeds by rapid stages toward stabilization. When lumbering is followed by fire or excessive erosion it may cause pronounced physical changes in the site and the progress toward stabilization is slow.

5. INITIAL CAUSES IN SUCCESSION

Sites are either originally bare or made bare by denudation. The underlying cause in the initiation of a secondary series is a bare area on which plants can become established. However, there must be an adjacent plant population from which migrants can come. Succession does not occur on a denuded area unless the denuding agent changes the site. This is particularly true of small burns where the surrounding vegetation is mobile. Clements (1910) has called attention to the fact that in certain lodgepole pine burns in the Rocky Mountains, firegrass, fireweed, aspen, and lodgepole pine appear together the first year after fire. Here also there is an apparent succession following expression of dominance on account of differences in rapidity of growth.

Physiography is very important in initiating both primary and secondary succession. The initial cause is physiographic when the succession starts in consequence of a change in topography. All the forces which mold land surfaces either add to the land or take away from it. Often the same agent does both, as illustrated when a stream erodes at its headwaters and deposits a delta at its mouth. The various processes which control topography and thus shape the surfaces available for succession are: erosion, deposition, flooding, drainage, elevation, and subsidence (Clements, 1916).

Climate may be important in initiating a secondary series through the action of drought, wind, snow, hail, frost, and lightning, in destroying vegetation, and in creating bare areas. Thus the initial cause is climatic when the series starts from denudation due to climatic or weather conditions which critically affect the water or heat relations of the plant community.

The initial cause is biotic when the series starts because an area has been made bare by living agencies. Thus when an animal or plant pest produces a bare area by killing all the plants of the community,

as sometimes occurs in forests growing in pure stands, the initial cause of the series is biotic. Sometimes the initial cause is destruction of vegetation by man. Lumbering does not usually initiate a series except when followed by fire or a long period of overgrazing. Complete denudation by animals is of infrequent occurrence. Beavers may initiate a series by damming the outlet of a lake, causing denudation by overflow and drowning of vegetation. A very destructive barkbeetle (*Dendroctonus frontalis*), common in the Southern Appalachian region, has killed shortleaf and pitch pines in groups and often over relatively large areas, hastening the normal succession from pine to hardwoods.

The entire course in succession depends upon the nature of the bare area which initiates it. Primary bare areas, such as rock surfaces, present extreme conditions; consequently the earlier stages in the succession require long-continued reactions before the site is ready for the climax stage. Secondary bare areas, such as recently tilled fields and alluvial deposits on floodplains, present less extreme conditions as they retain to a greater or less extent the advantages accruing from preceding reactions. They give rise to relatively short and simple stages.

6. CONTINUING CAUSES IN SUCCESSION

The continuing causes in succession are the causes which carry onward the series after it has once been set in motion by the initiating cause and which carry it forward to the climax form. Thus the initiating cause produces a bare area while a continuing cause delimits the vegetation, determines the sequence of stages, and terminates the development. The continuing causes are expressed in the responses and adjustments which vegetation makes to the site. For the most part they deal with vegetation itself rather than site and may be classed as processes by which:

1. Plants that enter the bare area tend to become grouped together.
2. Progeny of plants tend to move from a given plant community and become established in another.
3. Space requirements arise in a plant community.
4. Physical and to lesser extent biotic factors become so changed that the growth forms originally present give way to others.

7. PLANT GROUPING

Reproduction tends to group about a parent tree. Migration tends to dissipate it. Grouping usually operates by means of seeds; sometimes, however, as in certain willows, black locust, aspen, and ailanthus, by vegetative parts. Although in the fall of seed there is always some movement away from the parent tree, migration is not affected if the

movement is only within the limits of the plant community. Movement must go into outside communities if it is to become a factor in succession. The gradual increase in plant population on a site hitherto bare is mainly due to grouping. Jack pine and lodgepole pine, which hold their cones unopened for many years and shed the accumulated seeds of years after a fire, are striking illustrations of grouping. Here the series may begin and end with what are essentially family groups. It may start with a dense, pure stand of lodegpole pine seedlings and end with a pure stand without undergrowth. The development of groups of the same descent, however, is impossible where fire kills the seed, and vegetation which starts is through migration from outside. In instances where the seed is not destroyed by fire, as where covered by moist litter, and when buried by animals or protected by resistant fruits, vegetation that follows denudation is only partially a result of migrants from outside. Accumulating evidence appears to show that in the Pacific Northwest reproduction after denudation by fire is very largely from viable seeds brought in by the wind or by other agents from outside after the fire has taken place (Isaac, 1935, 1943).

8. Variety in Grouping

As soon as competition, either for crown space or root space, begins in a developing stand, the successive strata or layers in the vegetation undergo modifications and adjustments in order to adapt themselves to the changed conditions. The arrangement of forest vegetation in layers has been explained as a reaction to the different light requirements of the species. Absence of vegetation on the forest floor and absence of intermediate layers have been explained as the result of low light intensity and light of different quality beneath canopies. Present evidence, however, appears conclusive that the presence or absence of layers in the forest is not a response to light alone, but to other factors as well. When trees and other plants are brought together so that they are entirely independent of each other in respect to mechanical support or nutrition, they are said to be independently associated. When they derive support or nutrition one from the other they are dependently associated. Forest trees are independently associated in that they do not derive nutrition or mechanical support from each other. The result of the process of grouping is, however, to permit entrance of dependent species later on, as illustrated in parasites, epiphytes, and climbing vines. Grouping may result in either an open or a closed vegetation, depending on the frequency and size of individuals. When open, be-

cause of incomplete occupation of the soil, the vegetation is very unstable. When closed, complete occupation of the soil prevents the entrance of additional individuals without displacement of some already there. When open above ground, the vegetation may be stable or unstable, depending upon the degree to which the soil is occupied by roots. Thus ponderosa pine forests of Arizona and New Mexico are open above ground, yet in stable condition. When individual plants come together they group themselves in response to particular site factors.

9. Grouping in Response to Light and Moisture

When individual plants are of the same height and consequently on the same level, they are uniformly exposed to light. On the other hand, when they are not of the same height, they form groups of different heights or layers, each of which receives light of an intensity and quality different from that received by all others. This is a common characteristic of forest vegetation. In a forest of full density the direct light is largely intercepted by trees forming the upper layer.

Layers often disappear in dense even-aged coniferous forests because of response to decreased soil moisture. Thus the forest floor is completely clear of vegetation in white pine and spruce plantations in New England from an early age well on toward maturity. The same is also true of dense, even-aged natural stands of hemlock, lodgepole pine, and many other species. In these dense stands the vegetation is reduced to a single superior layer.

Although during dry periods a forest cover may reduce soil moisture below that of adjoining open land, recent studies by Shirley (1932) indicate that drought losses to secondary vegetation are likely to be less severe in forests. It appears that on dry upland soils the early stages of forest succession are marked by those species most capable of withstanding unfavorable moisture conditions, whereas in the later stages plants capable of remaining in vigorous condition for long periods of low light intensity tend to become dominant.

One of the most noticeable characteristics of vegetation is the grouping of plants in response to their demands for moisture, as expressed in water content of soil. Zonation of forest vegetation arises very often from the grouping of plants in response to water requirements. This is well illustrated in the concentric zones of vegetation surrounding lakes and ponds extending from the water's edge to the highest elevations from which the drainage enters a pond or lake.

10. Relation of Grouping to Structure in Forest Vegetation

An individual plant exhibits various structures, some of which are retained and contribute to its final form and others are transitory and disappear after they have performed their functions. In the same way plant communities exhibit structures in the course of development. All structures exhibited by plant communities can be referred directly to zonation, either horizontal or vertical, and indirectly to alternation (Clements, 1916).

11. **Zonation.** — Zonation is due to the gradual increase or decrease in effectiveness of a site factor, from an area of deficiency or excess. Thus zonation in vegetation at the margin of a pond is due to water relations. There is lateral zonation from the margin of the pond inland, and from the base of a slope to the top, because the soil becomes progressively drier and as a result exhibits a constant decrease in growth water. Altitudinal zonation is due to heat relations. Thus in the ascent of mountains the mean temperature is lowered about 1° F. for every 300 feet in elevation. As a result, in passage from lower to higher altitudes successive vegetation zones are encountered. Latitudinal zonation is also due to heat relations. In passing from the tropics toward the poles broad climatic zones of vegetation are encountered.

Zonation about a pond or lake is not only horizontal, but it may also be vertical; one zone may be superimposed on the other. Thus with the successive filling in of ponds, the vegetation of one zone comes to occupy the same spatial position as the vegetation of another zone but in the filled-in soil above the remnants of the old vegetation. Thus there is a vertical zonation of plant remains which is a repetition of the horizontal zonation of living vegetation. The usual vertical zonation or arrangement in layers in a forest is also due largely to water relations. In every forest where they are close enough to induce competition, individual plants arrange themselves in consecutive layers, one above the other. Thus close to the soil a layer of moss and lichens is found. Immediately above these is a layer of herbaceous vegetation. Above the herbaceous layer is one of shrubs, and still above this are one or more layers of trees. The absence of one or more subordinate layers is due to the intensity of competition.

In a dense coniferous forest the lowermost layer may at times have its roots exposed to but one-third to one-fifth as much available moisture as the roots of the uppermost layer. The subordinate layers must, therefore, disappear long before available soil moisture becomes critical for the upper layer. Although the differentiation of layers is a charac-

teristic of nearly all vegetation growing in closed stands, its most striking and typical development is in forests. An even-aged stand of pine, spruce, or hemlock may be so dense that practically all the layers beneath disappear. The layer of shrubs disappears first, followed by the layer of large herbs, and later by the low herbs. Mosses and lichens remain as a final remnant of the layered condition.

The layers in a deciduous stand are usually quite different from those in a coniferous forest. Deciduous forests have a vernal ground layer of low plants which develop before the other layers unfold their leaves. Thus many low plants develop and blossom in deciduous forests before the trees expand their foliage. They are entirely absent in coniferous forests.

12. **Alternation.** — Although zonation is a universal structural characteristic of vegetation, it is usually more or less completely obscured by alternation because of the heterogenous character of the soil surface and the disturbance of vegetation by denuding agents. Alternation is superimposed on zonation. The primary cause is the heterogeneity present in the broadly symmetrical areas which produce zones. Whenever the conditions which produce zones are disturbed, alternation results. This is illustrated where a shrub or forest community extends up a moist north slope or ravine but does not occur on dried areas which may be covered by a grass community.

13. PLANT MOVEMENT AND ESTABLISHMENT

The two processes in invasion are the actual movement of a plant from one community into another and its establishment there. The movement of plant descendants out of a given community is migration and their persistency in another community is establishment. Migration is a phase of succession closely related to plant grouping. Thus, if there is no dispersal the process of grouping is carried to the highest degree; if dispersal takes place, migration is effected. Migration is quite distinct from establishment, because migration takes place before establishment begins. Furthermore, migration is not always followed by establishment. Migration begins when the seed or other migrant leaves a given community and ends when it comes to rest in another.

Because of the attachment of trees to the soil during development and growth, their period of mobility is chiefly confined to the time when they are dormant in seeds. Many species are, however, more or less mobile at other times. Thus *Opuntia*, *Salix*, and various other genera include species adapted for vegetative dissemination (Toumey, 1895). Various species of *Fagus, Robinia,* and *Rhus* develop root-suckers which

ultimately become separate individuals; consequently they do not depend wholly on seed dissemination for mobility. Forest trees exhibit a wide range as to the degree of mobility in the seed. With species that are relatively immobile, owing to lack of adaptations for seed or vegetative dissemination, the result of reproduction is quickly to form a colony of individuals of the same descent about a parent tree. Mobile species do not usually originate grouping through reproduction because of their wide dissemination. Furthermore, when grouping is attained, it is more likely to be the assembling of individuals from many parents, and consequently is usually a mixture of species or from a mixed parentage within a single species. In general, it may be said that immobility promotes the bringing together of individuals, all of which are descendants of the same parents; whereas mobility promotes the assembling of individuals of mixed parentage. Because of the greater or lesser degree of mobility in all species, it is very seldom in nature that an association of individuals composed of successive generations from the same parents is found. Mobile species are continually migrating and becoming established in these family groups.

A forest community is seldom if ever composed entirely of plants which have developed distinct characteristics as a result of its own particular environment. Other plants are continually coming in through migration. Of the many species, however, which are continually entering every community through seed and vegetative dissemination, the great majority does not become established. The seeds do not germinate, or when they do the resulting individuals do not survive and reproduce. Certain species, however, even when they have moved in from sites having somewhat different site factors, have the inherent power to become adjusted to the new environment and, as a result, they become established and form a permanent part of the community. More often, however, they persist only during a certain period of development and are ultimately driven out to enter again when some disturbance of soil or vegetation makes it possible.

14. Migration

The factors which determine how many seeds or other migrants will be carried into an outside area are:

1. Degree of mobility in migrants.
2. Agency by which they are carried.
3. Nearness of parent area to the site into which they are carried.
4. Topography of intervening area.

15. Degree of Mobility in Migrants. — Mobility in tree seeds depends chiefly on their size and weight and on the configuration of their surfaces. The special structures that are found in the seeds of tree species that are aids in dissemination are very numerous and of great interest. In most instances they relate to distribution by wind, water, and animals. Where dissemination is effected by wind, the fruit or seed is so modified as to expose a comparatively large surface to wind action. Thus the seeds of conifers, as illustrated in larch, spruce, and most pines, are winged. The fruits of many broadleaved species are equipped with similar structures, as illustrated in birch, maple, and ash. In some species, the seeds are provided with fine, silky, capillary hairs which serve to buoy them up as illustrated in willow and aspen. Where dissemination is accomplished by animals, the seeds or fruits are provided with some means of attachment, such as hooks, barbs, and spines or by a viscid outer covering, or else they are used by the animal as a source of food. When used as a source of food, as is illustrated in walnut, hickory, oak, chestnut, and beech, the surplus fruits that are not eaten are carried away and buried in the ground; later some of them germinate and become established. In cherry, black gum, and dogwood only the fleshy outer part of the fruit is digested. The seed and the contained embryo remain uninjured because of resistance of the endocarp or the seed coats to digestion.

As a rule, species that produce seeds in large numbers are highly mobile, as illustrated in the various species of birch, sycamore, and willow. On the other hand, trees which produce a relatively small number of seeds are relatively immobile, as species of walnut, oak, and chestnut. In these species, however, the degree of viability is usually much higher, as shown by black walnut which has an average viability of 85 to 95 percent as contrasted with sycamore which has an average viability of 5 to 10 percent.

The periodic variation in seed production is very important in migration. Thus with many conifers, oak and beech, the time of invasion depends upon the occurrence of good seed years, which may be at intervals of 3 to 12 years.

16. Agents for Carrying Migrants. — The agents of distribution are determining factors in migration because, without them, the most perfect contrivances for mobility in the seeds or vegetative parts are useless; the migrants can not be carried into new areas. The important agents in migration affecting succession in forests are: wind, water, gravity, glaciers, slides, animals, and man. These may also be

initial causes of bare areas, and the agent which causes denudation may bring the new population to it. Sometimes the two go along simultaneously; thus moving water, which causes denudation by erosion, deposits on the denuded area seeds which it gathers along its course. Also the agents which transport the seeds determine how large a proportion will reach the new area in viable condition. The action of water is destructive to some species but favorable to others. Large numbers of seeds are covered up in deposits from eroded material. Animal life is both an agent of distribution and of destruction. Seed-eating birds and rodents are often a determining factor in migration, owing to the large number of seeds destroyed by them. So complete is the destruction of seed in certain instances that the species reappear on denuded areas only after the seed-eating animals are driven out or destroyed. Although chestnut fruits abundantly, the seeds are so completely destroyed by insects and rodents that their dissemination is a matter of minor importance. In some parts of Montana the destruction of seed in lodgepole pine forests is so complete that it profoundly affects migration. Direct seeding in reforestation often fails, because of destruction of the seed; and it can not be successful without first destroying the seed-eating animals.

The agencies through which migration is effected are in some instances constant, as when the distributing force is wind, water, or gravity. Other agents are inconstant or intermittent, as animals or man. With the constant agents, migration is likely to be more determinate and in fixed directions; with the inconstant ones it is variable as to direction and time, and its abundance and distance over which it extends may be greater though less frequent.

Wind is the foremost agent in effecting dissemination of forest-tree seeds. This is particularly true of coniferous species, the greater number of which have special adaptations for dispersal by wind. Also many broadleaved trees, as illustrated in species of cottonwood, birch, sycamore, ash, and maple, have fruits or seeds provided with adaptations for wind dissemination.

Water is an important factor in effecting the dissemination of all fruits and seeds that will float. It is also important in the dissemination of the vegetative parts of plants, which after being carried for variable distances, take root and become established. It is of the most importance in effecting the migration of those species that grow on the banks of streams and the borders of lakes. As a rule, special modification in the form of fruit or seed is not essential for water distribution. The only requirement is that they float for considerable

periods without becoming water-logged and sinking to the bottom. Fruits of river birch and elm are often carried in large numbers and for long distances on the surface of moving water and are finally left on moist banks in excellent condition for germination.

Gravity aids in migration only in mountainous and hilly regions where fruits and seeds, when they fall to the ground, roll or are otherwise carried by gravity to lower levels. In the hilly regions about New Haven, Connecticut, and in the southern Appalachian Mountains, the authors have observed the accumulation of chestnut oak acorns in large numbers at the foot of steep declivities. The acorns had been transported by gravity from far up the slope.

It is chiefly in alpine regions that migration is aided by glaciers and slides. Sometimes, however, slides occur at lower elevations which carry with them seeds and vegetative parts capable of establishment.

Animals that feed on the fruits and seeds of various tree species occur in every forest. In some instances the fruit has a fleshy outer part, as black cherry and red cedar, which are relished as food. The hard seeds pass through the animals undigested and are deposited often many miles from their place of origin. Squirrels and rodents carry away and bury for later use many fruits and seeds, all of which are not eaten by the animals. The striking characteristic of migration through the agency of animals is the great distance to which seeds are carried, thus bringing about the introduction of species into areas at long distances from their place of origin.

Man's chief activity in effecting migration is in the transportation of seeds and vegetative portions of plants over railroads, roads, highways, trails, and airplane routes, and the scattering of seed and the planting of vegetative parts.

17. Nearness of Parent Area to New Locality. — Except in cases where man, either directly or indirectly, is the agent through which migration is effected, nearness of the new locality to the parent area is an important factor in migration. In all other cases the operation of modifications to attain movement and of the moving agent is influenced by distance. The greater the distance, the less likely it is that migration will be attained. There are few available data regarding the frequency of migration in various tree species depending upon distance from parent trees. In all species the greater number of seeds reach the ground within a few hundred feet of their source. This is clearly shown in the fact that white pine and red pine seldom seed areas in sufficient quantity to form a stand at a greater distance than 200 or 300 feet from the mother trees. Red spruce and eastern hemlock seedlings

dense enough to form a satisfactory stand are usually found within 450 feet of mature timber in West Virginia (Korstian, 1937). The seeds transported to greater distances become fewer and fewer with increase in distance until finally migration is entirely excluded. The maximum distance that the seeds of different species are carried depends very largely, however, upon special circumstances. For instance, in wind-disseminated species, the distance seeds are carried depends upon the frequency of storms in which the wind attains high velocity during the period of seedage (Siggins, 1933). When under normal conditions the seeds would be carried only a few hundred feet at most, under special conditions they might be carried several miles.

18. Topography of Intervening Country. — Topography, by affecting wind and water and other agents of distribution, indirectly influences migration. Thus seeds are carried by wind much longer distances over treeless, level country than over broken, hilly regions. In mountain regions where the topography is bold and broken, numerous streams have high velocity and carry seeds for long distances in comparatively short periods of time. On the other hand, the sluggish flow of streams in flat country is usually an unimportant factor in seed dispersal. McAtee (1925) has shown, however, that floating river and lake drifts often carry large numbers of tree seeds. Even the large seeds of hickory, oak, and beech are reported in river drift.

19. Direction of Movement. — Migration is seldom, if ever, uniform in every direction from the parent area. The presence of natural reproduction in a given direction from a parent tree is generally an index of direction of migration. Direction of migration is controlled by the distributing agents; establishment is controlled by the factors which make survival possible. With wind-disseminated species, which include a large number of valuable timber trees, direction of dissemination is determined by direction of the prevailing wind at time of seedage. It is for this reason that in leaving seed trees special attention should be given to the position that they occupy in relation to the open spaces. It also may determine the direction and location of clear cuttings with reference to the remaining stands. Migration effected through the agency of man follows the great commercial routes; with animal life it follows the general routes of animal migration.

20. Establishment. — After migration has become effected by the transport of seeds into new areas, invasion is not completed unless the invaders germinate, grow, and reproduce. They must adjust themselves to the new site and become established. Seeds of forest trees are carried yearly beyond their areas of local occurrence and even beyond

their natural ranges. In most instances, however, establishment does not result, because the site factors in the new region are dissimilar to those from which the migrants came. The greater the divergence, the less likelihood that the plants that result from migration will mature and reproduce. Distance in establishment is of consequence only insofar as it affects the site factors. Establishment sometimes occurs at great distances from the parent area, as when trees are introduced by man. This is illustrated in European bird cherry and white mulberry which are fully established in many places in the eastern United States. Other barriers which exclude establishment may arise within a few rods. Of the various species which in the seed reach a given area through migration, some do not germinate, others germinate but soon disappear, others grow and mature but do not reproduce, and others reproduce. Only the last are true invaders. Establishment does not occur except when germination and growth are followed by reproduction. Scattered individuals often occur beyond the borders of their areas of distribution as a result of migration followed by germination and growth. Because of lack of reproduction, however, they soon disappear. They are fugitives in the plant community in which they occur. They make no permanent imprint on it. Establishment, which embodies germination, growth, and reproduction, necessitates the adjustment of an emigrant to its new home. Adjustment makes migration effective through establishment. It is the decisive factor in invasion.

21. Germination. — The first critical process in establishment is germination. It regularly occurs when viable seeds meet favorable conditions as to water, heat, oxygen, and sometimes light. The time required, however, varies greatly with different species, and with condition of the seed. In willow, for instance, it is measured in hours; in other trees, as red cedar, it is measured in years. There is also great variability in time within the same species and the same lot of seed. The normal period of viability in tree seeds under the most favorable and under the most unfavorable natural conditions is unknown for nearly all American species. To a considerable extent it appears to be a function of permeability of seed coats or pericarp, but in some species it appears to be inherent in the embryo, mature seeds requiring a more or less extended period of after-ripening before germination will take place.

When seeds are carried into new areas germination is determined by the nature of (1) the site and (2) the seeds themselves.

The influence of the site is probably of far more importance than is generally believed and is not wholly dependent on heat and moisture. The conditions for germination are usually better under cover than in

the open. In nursery work seed beds are covered because of the effect of shade on the heat and moisture conditions of the surface soil and as a consequence on germination and early growth. Although the conditions for germination are usually best under canopies, an overly deep litter of either coniferous or hardwood leaves is unfavorable. Exposed mineral soil beneath canopies is most favorable.

Condition of the site determines where germination will proceed as soon as the migrants reach their resting place or whether it will be delayed. When germination is delayed, the site also determines how long seeds can lie dormant without losing their viability.

As a rule, sites that are most favorable for germination are least favorable for storage of seed. With the exception of bare areas with wet or moist surfaces, germination in the open is measured by depth of soil covering. The effect of the covering is to render moisture conditions more uniform. Too great a depth of cover, however, delays germination, or causes it to appear in abnormal form, or not at all. Hofmann's (1924) researches show that of selected, large, fresh seed of ponderosa pine covered to a depth of 1 inch, 82 percent germinated and appeared above ground, whereas a portion of the same lot of seed covered to a depth of 4 inches germinated only 36 percent, none of which appeared above ground. In Douglas fir, 93 percent germinated and appeared when covered to a depth of ½ inch, but only 17 percent germinated at a depth of 4 inches and none appeared above ground.

Length of time between dissemination and germination is a significant factor in the probability of germination, because it is a measure of the likelihood of injury or destruction by outside agents. Seeds that require a year or longer to germinate usually produce only scattered elements in a given vegetation. They are largely destroyed. On the other hand, seeds that germinate shortly after migration has been effected usually produce the abundant elements in a given vegetation. There is great variability in a given species in length of time that seeds lie dormant, even when they are from the same parent or from individuals grown under similar conditions as to site factors. Even with species of maple, which usually germinate with the first warm days of spring, a small percentage of seed remains dormant until the second year even when subjected to uniform conditions. Different species of forest trees vary greatly in percentage of seed carried over to the second or third season. Under suitable storage conditions seeds of American elm and red maple, which mature in late May or early June and which usually germinate immediately after ripening, can be carried over until the following spring (Toumey and Korstian, 1942).

22. Growth and Development. — Probably in all cases the most crucial period in adjustment processes is reached when a seedling is freed from the seed coats, and the young plant is thrown upon its own resources for food and protection. Of the thousands of tree seeds that germinate, only a few of the resulting seedlings grow and become established. Some are destroyed by grazing animals and others by insects. The high temperature of the surface soil destroys vast numbers. Damping-off fungi and other plant parasites take their toll. Herbs and other vegetation crowd in upon them and destroy them by excessive competition for growing space. The fate of tree seedlings is largely determined during the first growing season. Depth of penetration of root system must keep pace with downward desiccation of soil during the driest periods of summer and autumn. Form of root system is often decisive in determining establishment. Shreve (1911) found in southern Arizona that the mortality of seedlings of palo verde was 70 percent during the first year and 97 percent by the end of the third year. The senior author in 1899 found the mortality of seedlings of ponderosa pine in the San Bernardino Mountains of southern California to be more than 99 percent during the first year. This was due to high temperature of surface soil and to root penetration not keeping pace with depth of soil desiccation because of summer drought. Intensive studies of natural reproduction of this species in Arizona indicate that there also infant mortality is generally so high that, time and again, promising stands of young seedlings have been almost completely wiped out during the first or even the second season (Pearson, 1923).

After germination has taken place the ability of a migrant to grow and mature depends upon the similarity of the old and the new sites and its inherent power for adaptation to new site conditions. The range of accommodation in American tree species to different site conditions is in most instances within rather narrow limits. Germination of the migrants of a given species may occur on sites that are widely different. Thus in southern New England, yellow birch is a typical swamp species. The widely disseminated seeds, however, germinate in large numbers on uplands, but the seedlings soon disappear because of their shallow root systems. Seeds of gray birch germinate in large numbers under the canopy of hardwood forests but the seedlings soon disappear in competition. In general, it may be said that xerophytes do not become adjusted to wet sites and hydrophytes to dry sites. Intolerant species do not become adjusted to the deep shade of a dense overstory, owing to competition. The probability of adjustment is usually greater in intermediate forms. Thus mesophytes are more likely to become adjusted to either wet or dry sites, and species intermediate in tolerance

are more likely to adjust themselves either to the deep shade of an overstory or to full sunlight.

Physical barriers of one kind or another, such as high mountains and broad stretches of desert, often prevent growth and development after migration has been effected, primarily because of marked changes in site factors. Thus, in the isolated mountain ranges of Arizona, the surrounding desert sets a limit to the spread of mesophytic forest vegetation, although seeds are carried in abundance in all directions far beyond the limits of the mountain areas. Vegetation of one type or another may act as a barrier to establishment after germination has been effected. Thus a dense forest is an effective barrier to intolerant species. All closed formations, because of competition, are more or less effective barriers. Tree seedlings that survive the first year are fairly certain to continue growth until crowded out by competition or destroyed by fire or other occasionally destructive agents. Some species emerge from the competition as dominants and in time determine the conditions for all other species in a community.

23. Reproduction. — A migrant does not become a permanent part of the vegetation of a new area by germination and growth alone. It must mature and reproduce. Many species enter tree communities only to remain a few years or through the life of the individual migrants. They do not find the environmental conditions favorable for reproduction, true of most forest trees when carried far beyond the limits of their continuous reproduction. They may be able to grow and mature but are not able to flower or produce fertile seeds. Thus in southern Connecticut invasion by persimmon is only of temporary character because the migrants do not produce fertile seeds. Species which have become established in a plant community during its process of development are derived vegetation. In every community the derived elements exhibit a variable degree of permanency. Some become fully established, even when they come from distant sites. Others are not able to establish themselves permanently. Establishment occurs only when the species persist generation after generation.

24. Competition and Reaction

When migrants enter a new site they find it bare, or else there are occupants of the same species or of different species already there. As to the degree of occupation, sites are:

1. Naked, that is, without a vegetation cover.
2. Open, that is, with a vegetation cover, but with the individuals so far apart they do not react upon each other.

3. Closed, that is, with a vegetation cover so dense that the individuals react upon each other to their advantage or disadvantage.

Naked sites, such as dunes and talus slopes, although offering ample space for establishment, often present very adverse conditions, such as pronounced dryness and soil instability. Denuded sites, on the other hand, as abandoned fields and burns, afford excellent opportunities for establishment, not only because of ample space but also because they provide suitable soil conditions as to moisture and nutrients. Establishment is most easily attained in open communities. In closed communities, establishment is very difficult, because of unfavorable conditions resulting from their density.

25. Competition. — Competition may be said to occur whenever two or more occupants of a site make demands on site factors in excess of the supply. It appears in a plant community as soon as the elements of vegetation pass out of the stage of isolation and it increases in intensity with the increase in plant population in the various stages in succession until the climax stage is reached. Competition is always greatest between individuals and species that make the same demands on site factors and at the same times. Thus competition is usually keenest between individuals of the same species. It is least between plants whose demands on site factors are quite unlike. Species that can best resist adverse conditions of the site, or are best adapted to it, are naturally those that take possession when in competition with other species. Competition does not exist between the host and its parasite. Competition in forests is most apparent when water available for each individual or for each species is decreased over that which it receives when isolated. Dominance is shown best in the development of a many-storied forest. In the early stages of succession, after a community closes, all individuals compete with each other. As soon as shrubs appear they become dominant and form a layer above the herbs. Later trees become dominant and form a story over the shrubs. Each of the subordinate stories is adjusted to those above. Within the over-story individual trees and species compete with each other. The elements of this layer, however, were in competition with those of the subordinate layers when they were members of those layers.

26. Competition for Moisture. — Competition for moisture expresses itself in forests in the arrangement of roots below ground in accordance with their requirements for moisture. Individuals and species are competitive when their roots occupy the same soil layer and draw their water supply from it.

A plant community may be composed of individuals entirely isolated

in the parts above ground, and without competition for light, as in the open stands of short spherical-crowned trees on the low mountains of southern Arizona. The same community, however, may exhibit intense competition for moisture in the parts below ground. In a sense the community is closed because no additional individuals can enter it without forcing out some already there. It is open above ground but closed below. Such a community is stable, although individuals may be isolated in the parts above the soil surface.

27. Importance of Competition. — The effect of competition upon the adjustment of vegetation to new sites is direct and determinative, because it affects light and water relations, often to a point of complete control as soon as competition results in dominance. Competition is more or less effective in all plants at the time of germination and during the development of seedlings, particularly during the first year. It is effective in arborescent species during the period of principal height growth. It plays a prominent part in determining the number of occupants in each stage in succession and the number of invaders that can enter. The controlling influence of competition in the different stages in succession is illustrated as follows: The first stage following complete denudation by fire is a surface layer of lichens and moss with scattered pioneer seed plants. However, no competition occurs between them, owing to their dissimilar demands on site factors. Competition begins with an increase in population to the point where they deprive each other of adequate light, moisture, and nutrients (Clements, Weaver, and Hanson, 1929). Invaders continue to enter and in time they so react on the site that the first occupants are driven out. In southern New England gray birch usually enters before the grasses and other herbaceous perennials become controlling, and competition passes into the dominance of gray birch. White pines often enter before gray birch becomes controlling and during the period of its development. They increase in number and enter into vigorous competition with the birch as soon as their crowns enter the same crown class as the birch. The pines ultimately attain complete dominance and the birches disappear. As soon as dominance is attained, the pines compete with each other and on the better soils cause reactions unfavorable to their seedlings but more favorable to the seedlings of sugar maple, beech, and other hardwoods. In competition which ensues during the seedling and sapling stages the latter succeed and in time take their places in the upper story as codominants. Pines decrease in number and hardwoods increase, until the pines appear only occasionally and the climax stage is attained.

28. Reaction. — The effect which vegetation has on the site is known as reaction. It relates entirely to the site and is distinct from adjustment, which relates to the vegetation. Site factors cause vegetation to function and develop and it in turn reacts on the factors, causing one or more of them to change sufficiently to be decisive in bringing about a new stage in succession. The direct reactions of vegetation on the site affects both physical and biological factors. Although a tree as an individual produces reactions on the site, the reactions are recognizable only through the combined action of the plant community. Many illustrations can be drawn from forests to show the reaction of vegetation on the site. One hundred trees when assembled in a closed stand cast less shade than the same number growing as isolated individuals. Although they cast less shade, they cast a denser and more continuous shade and hence they control the vegetation, as the widely spaced trees do not. The reaction of trees on wind is chiefly felt where vegetation is in closed stands. So also the reaction of vegetation, because of litter and humus, is chiefly a function of stands, not of isolated trees. Reaction begins only after the first pioneers on a denuded site have become adjusted to the new conditions. Vegetation that starts after denudation sometimes produces a closed community the first year and reaction begins at once. Reaction of vegetation on the site makes succession possible. It provides an explanation of the orderly development of all vegetation by stages, from the initial to the climax.

29. Classification of Reactions. — Reactions of vegetation on the site may be classed in two groups in accordance with the location of the reaction:

1. Soil reactions.
2. Air reactions.

30. Soil Reactions. — As soil is more or less fixed and air is not, the former is much more affected by vegetation. The reactions of vegetation on soil are much more numerous and of greater importance than those on air. The soil reactions may be grouped in accordance with the edaphic factor directly affected, as follows:

1. Soil formation and structure.
2. Water content.
3. Solutes.
4. Soil organisms.

The reactions of vegetation on soil formation relate to those which produce a new soil and those which affect the old soil. Vegetation forms new soil chiefly through the accumulation of dead plants and by

the resistance which it offers to soil transport; also by excretions of roots which break down rocks. Plants modify soil by changing its texture through their death and decay and also to some extent by depth of root penetration. On certain soils like heath sands, humus solutes may be carried in the soil water down through the surface layers of sand (Weis, 1932). When they reach the deeper layers richer in salts they may be precipitated and bind the particles of soil together into a kind of hardpan. So long as the hardpan persists, succession may terminate in a heath community which is climax for the site.

Vegetation reacts on water content by increasing it in the surface layers of soil, chiefly through accumulation of humus and litter. It increases the water content of soils, particularly at times of drought, through the effect of a living cover and litter on evaporation. Vegetation decreases the water content through transpiration.

The reaction of vegetation on the soil solution relates to its effect in both increasing and decreasing the soil nutrients and to the production of toxins. Thus the annual fall of leaves through their decay augments the soil nutrients, and absorption of nutrients through roots diminishes the supply in the soil. To what extent soil toxins are excreted by plant roots is not definitely known. Vegetation reacts upon an indefinite number of soil organisms, both plant and animal, and profoundly affects soil fertility.

31. RECOGNITION OF THE CLIMAX IN SUCCESSION[1]

The climax is the mature or adult stage in succession. It is the fully developed tree community. Recognition of the climax is necessary in the study of the development of forest vegetation. The climax is reached when the occupation and reaction of dominant growth forms prevent the establishment of other dominant growth forms. Thus in a stand where beech and maple are the dominants they effectively prevent the entrance of other species as dominants in New England; hence beech and maple are the climax. Although the climax marks the close of the development, it is often difficult to recognize and can be interpreted only by a careful study of all stages in succession over the entire climatic unit area where dominants of the same growth forms exist.

32. DIRECTION TAKEN BY SUCCESSION: RETROGRESSION

Ordinarily succession proceeds in an orderly manner from a bare area to the climax. The course of development may be hastened or

[1] The climax concept has been developed in considerable detail by Clements (1916, 1920, 1928, 1936), Weaver and Clements (1938), and Phillips (1934, 1935).

prolonged and it may be interrupted or deflected from its normal course. This forward movement may be upset by the activity of denuding agents of one kind or another and sometimes this is taken for retrogression in the succession and the plant community seems to have degenerated. This apparent degeneration is caused by destruction of the plant community in varying degrees by the denuding agent, but the moment the agent ceases succession proceeds in a normal manner. The early stages in a secondary succession produced by denuding or degenerating agents give the appearance of retrogression. Development usually begins anew on the area at a point determined by the degree of denudation, and proceeds toward the climax, although a subclimax community may give way very slowly (perhaps only a few feet in 100 years) to the competition of invading species from an adjoining true climax type.

Retrogression from forest to scrub or bushland is explained by Tansley (1911) as follows: "The different types of plant community on the same soil, namely, scrub or bushland, and a corresponding grassland or heathland, have no doubt originated mainly from the clearing of the woodland, and of most of the shrubs also, if the pasturage is sufficiently heavy and continuous, while it encourages the growth of grasses. Thus the plant formation determined by the particular soil, and once reforested by woodland, shows a series of phases of degeneration or retrogression from the original woodland, brought about by the activity of man."

The researches of Gräbner (1901) appear to show that a forest may be replaced by heath or moor by changes in the forest climax. A calcareous soil bears a beech forest which is completely removed as a consequence of the great demand for wood. While the ground remains bare and the forest slowly renews itself, the leaching-out of nutrients in the soil proceeds. Finally the forest again becomes closed, then matures, and is again cut down. This may recur several times, during which the leaching-out of nutrients in the upper layers progresses steadily. With the decrease of moisture and nutrients in the upper layers, the growth of herbs and tree seedlings is made more and more difficult, and finally these die out, since their roots are unable to reach into the deeper undisturbed layers. In time the site is left to heath plants. However, following amelioration of the unfavorable soil conditions many of the Danish heaths can be reforested successfully (Weis, 1932).

APPENDIX

COMMON AND TECHNICAL NAMES OF TREES[1]

Common name	*Technical name*
Ailanthus	*Ailanthus altissima* (Mill.) Swing.
Alder, [European] black	*Alnus glutinosa* (L.) Gaert.
Alder, red	*Alnus rubra* Bong.
Alder, speckled	*Alnus incana* (L.) Willd.
Arborvitae, oriental	*Thuja orientalis* L.
All-thorn	*Koeberlinia spinosa* Zucc.
Ash, black	*Fraxinus nigra* Marsh.
Ash, blue	*Fraxinus quadrangulata* Michx.
Ash, European	*Fraxinus excelsior* L.
Ash, green	*Fraxinus pennsylvanica lanceolata* (Borkh.) Sarg.
Ash, pumpkin	*Fraxinus profunda* Bush
Ash, red	*Fraxinus pennsylvanica* Marsh.
Ash, water	*Fraxinus caroliniana* Mill.
Ash, white	*Fraxinus americana* L.
Aspen	*Populus tremuloides* Michx.
Aspen, largetooth	*Populus grandidentata* Michx.
Basswood	*Tilia* spp.
Bay, red	*Persea borbonia* (L.) Spreng.
Bay, sweet	*Magnolia virginiana* L.
Beech	*Fagus grandifolia* Ehrh.
Beech, blue	*Carpinus caroliniana* Walt.
Beech, European	*Fagus sylvatica* L.
Bigtree	*Sequoia washingtoniana* (Winslow) Sudw.
Birch, [European] silver	*Betula verrucosa* Ehrh.
Birch, gray	*Betula populifolia* Marsh.
Birch, paper	*Betula papyrifera* Marsh.
Birch, river	*Betula nigra* L.
Birch, sweet	*Betula lenta* L.
Birch, yellow	*Betula lutea* Michx.
Blolly	*Torrubia longifolia* (Heimerl) Brit.
Boxelder	*Acer negundo* L.
Butternut	*Juglans cinerea* L.
Buttonwood	*Conocarpus erecta* L.
Canotia	*Canotia holacantha* Torr.
Catalpa, hardy	*Catalpa speciosa* Warder
Cedar, Alaska	*Chamaecyparis nootkatensis* (Lamb.) Sudw.

[1] The terminology used for North American species is largely that of Sudworth, G. B. 1927. "Check List of the Forest Trees of the United States: Their Names and Ranges," U. S. Dept. Agr. Misc. Circ. 92. 295 pp. The technical names for exotic species are mostly from the Index Kewensis.

Cedar, eastern red .... *Juniperus virginiana* L.
Cedar, incense .... *Libocedrus decurrens* Torr.
Cedar, northern white .... *Thuja occidentalis* L.
Cedar, Port Orford .... *Chamaecyparis lawsoniana* (A. Murr.) Parl.
Cedar, Rocky Mountain red .... *Juniperus scopulorum* Sarg.
Cedar, southern red .... *Juniperus lucayana* Brit.
Cedar, southern white .... *Chamaecyparis thyoides* (L.) B. S. P.
Cedar, western red .... *Thuja plicata* D. Don.
Cherry, black .... *Prunus serotina* Ehrh.
Cherry, [European] bird or sweet *Prunus avium* L.
Cherry, pin .... *Prunus pennsylvanica* L. f.
Chestnut .... *Castanea dentata* (Marsh.) Borkh.
Cottonwood, black .... *Populus trichocarpa* Hook.
Cottonwood, eastern .... *Populus deltoides* Marsh.
Cottonwood, swamp .... *Populus heterophylla* L.
Cypress, Arizona .... *Cupressus arizonica* Greene
Cypress, Monterey .... *Cupressus macrocarpa* Gord.
Cypress, pond .... *Taxodium ascendens* Brongn.
Cypress, southern .... *Taxodium distichum* (L.) Rich.
Dogwood .... *Cornus florida* L.
Dogwood, Jamaica .... *Ichthyomethia piscipula* (L.) Hitchc.
Elm, American or white .... *Ulmus americana* L.
Elm, cedar .... *Ulmus crassifolia* Nutt.
Elm, English .... *Ulmus campestris* L.
Elm, red .... *Ulmus serotina* Sarg.
Elm, rock .... *Ulmus racemosa* Thomas
Elm, slippery .... *Ulmus fulva* Michx.
Elm, winged .... *Ulmus alata* Michx.
Eucalyptus or eucalypts .... *Eucalyptus* spp.
Fig, wild .... *Ficus brevifolia* Nutt.
Fir, alpine .... *Abies lasiocarpa* (Hook.) Nutt.
Fir, balsam .... *Abies balsamea* (L.) Mill.
Fir, California red .... *Abies magnifica* A. Murr.
Fir, corkbark .... *Abies arizonica* Merriam
Fir, Douglas .... *Pseudotsuga taxifolia* (LaMarck) Brit.
Fir, [European] silver .... *Abies pectinata* DC.
Fir, lowland white or grand .... *Abies grandis* Lindl.
Fir, noble .... *Abies nobilis* Lindl.
Fir, silver .... *Abies amabilis* (Loud.) Forbes
Fir, southern balsam .... *Abies fraseri* (Pursh) Poiret
Fir, white .... *Abies concolor* Lindl. & Gord.
Gum, black .... *Nyssa sylvatica* Marsh.
Gum, red or sweet .... *Liquidambar styraciflua* L.
Gum, swamp black .... *Nyssa biflora* Walt.
Gum, tupelo .... *Nyssa aquatica* L.
Gumbo-limbo .... *Bursera simaruba* (L.) Sarg.
Hackberry .... *Celtis occidentalis* L.
Hawthorn .... *Crataegus* spp.
Hemlock, eastern .... *Tsuga canadensis* (L.) Carr.

Hemlock, mountain	*Tsuga mertensiana* (Bong.) Sarg.
Hemlock, western	*Tsuga heterophylla* (Raf.) Sarg.
Hickory, bigleaf shagbark or shellbark	*Hicoria laciniosa* (Michx. f.) Sarg.
Hickory, bitternut	*Hicoria cordiformis* (Wang.) Brit.
Hickory, hammock	*Hicoria ashei* Sudw.
Hickory, mockernut	*Hicoria alba* (L.) Brit.
Hickory, nutmeg	*Hicoria myristicaeformis* (Michx. f.) Brit.
Hickory, pignut	*Hicoria glabra* (Mill.) Sweet
Hickory, red or pignut	*Hicoria ovalis* (Wang.) Sudw.
Hickory, sand or pignut	*Hicoria pallida* Ashe
Hickory, shagbark	*Hicoria ovata* (Mill.) Brit.
Hickory, southern shagbark	*Hicoria carolinae-septentrionalis* Ashe
Hickory, water	*Hicoria aquatica* (Michx. f.) Brit.
Holly	*Ilex opaca* Ait.
Hop-hornbeam	*Ostrya virginiana* (Mill.) Koch
Hornbeam, European	*Carpinus betulus* L.
Horsebean	*Parkinsonia aculeata* L.
Indigo bush	*Dalea spinosa* Gray
Inkwood	*Exothea paniculata* (Juss.) Radlkofer
Juniper, alligator	*Juniperus pachyphloea* Torr.
Juniper, California	*Juniperus californica* Carr.
Juniper, one-seeded	*Juniperus monosperma* (Engelm.) Sarg.
Juniper, Utah	*Juniperus utahensis* (Engelm.) Lemm.
Juniper, western	*Juniperus occidentalis* Hook.
Larch, alpine or Lyall's	*Larix lyallii* Parl.
Larch, European	*Larix europaea* DC.
Larch, western	*Larix occidentalis* Nutt.
Locust, black	*Robinia pseudoacacia* L.
Locust, honey	*Gleditsia triacanthos* L.
Magnolia, cucumber	*Magnolia acuminata* L.
Magnolia, evergreen	*Magnolia grandiflora* L.
Magnolia, umbrella	*Magnolia tripetala* L.
Mangrove	*Rhizophora mangle* L.
Maple, English field	*Acer campestre* L.
Maple, Norway	*Acer platanoides* L.
Maple, red	*Acer rubrum* L.
Maple, silver	*Acer saccharinum* L.
Maple, sugar	*Acer saccharum* Marsh.
Maple, sycamore	*Acer pseudoplatanus* L.
Mastic	*Sideroxylon foetidissimum* Jacq.
Mesquite	*Prosopis juliflora* (Sw.) DC.
Mulberry, [European] white	*Morus alba* L.
Mulberry, red	*Morus rubra* L.
Oak, bear or scrub	*Quercus ilicifolia* Wang.
Oak, black	*Quercus velutina* LaMarck
Oak, blackjack	*Quercus marilandica* Muenchh.
Oak, bluejack	*Quercus cinerea* Michx.
Oak, bur	*Quercus macrocarpa* Michx.

Oak, canyon live	*Quercus chrysolepis* Liebmann
Oak, chestnut	*Quercus montana* Willd.
Oak, chinquapin	*Quercus muehlenbergii* Engelm.
Oak, [European] pedunculate	*Quercus pedunculata* Ehrh.
Oak, [European] sessile	*Quercus sessiliflora* Salisb.
Oak, [European] turkey	*Quercus cerris* L.
Oak, laurel	*Quercus laurifolia* Michx.
Oak, live	*Quercus virginiana* Mill.
Oak, northern red or red	*Quercus borealis* Michx. f.
Oak, overcup	*Quercus lyrata* Walt.
Oak, pin	*Quercus palustris* Muenchh.
Oak, post	*Quercus stellata* Wang.
Oak, Rocky Mountain white or Gambel's	*Quercus utahensis* (DC., A.) Rydb.
Oak, scarlet	*Quercus coccinea* Muenchh.
Oak, Shumard red	*Quercus shumardii* Buckl.
Oak, southern red	*Quercus rubra* L.
Oak, swamp chestnut	*Quercus prinus* L.
Oak, swamp white	*Quercus bicolor* Willd.
Oak, Texas red	*Quercus texana* Buckl.
Oak, turkey	*Quercus catesbaei* Michx.
Oak, water	*Quercus nigra* L.
Oak, white	*Quercus alba* L.
Oak, willow	*Quercus phellos* L.
Osage-orange	*Toxylon pomiferum* Raf.
Palm, royal	*Roystonea regia* (HBK.) Cook
Palm, thatch-	*Thrinax* spp.
Palm, thatch-	*Coccothrinax jucunda* Sarg.
Palmetto, cabbage	*Sabal palmetto* (Walt.) R. & S.
Palo-verde	*Cercidium torreyanum* (Wats.) Sarg.
Pecan	*Hicoria pecan* (Marsh.) Brit.
Persimmon	*Diospyros virginiana* L.
Pigeon-plum	*Coccolobis laurifolia* Jacq.
Pine, Arizona	*Pinus arizonica* Engelm.
Pine, Austrian	*Pinus nigra* Arnold
Pine, bristlecone	*Pinus aristata* Engelm.
Pine, Coulter	*Pinus coulteri* D. Don.
Pine, digger	*Pinus sabiniana* Dougl.
Pine, foxtail	*Pinus balfouriana* Murr.
Pine, jack	*Pinus banksiana* Lamb.
Pine, Jeffrey	*Pinus jeffreyi* "Oreg. Com."
Pine, knobcone	*Pinus attenuata* Lemm.
Pine, limber	*Pinus flexilis* James
Pine, loblolly	*Pinus taeda* L.
Pine, lodgepole	*Pinus contorta* Loud.
Pine, longleaf	*Pinus palustris* Mill.
Pine, Mexican white	*Pinus strobiformis* Engelm.
Pine, Monterey	*Pinus radiata* D. Don.
Pine, northern white or white	*Pinus strobus* L.

Pine, Norway or red .... *Pinus resinosa* Sol.
Pine, pitch .... *Pinus rigida* Mill.
Pine, pond .... *Pinus rigida serotina* (Michx.) Loud.
Pine, ponderosa or western
  yellow .... *Pinus ponderosa* Laws.
  (Rocky Mountain form) ...... *Pinus ponderosa scopulorum* Engelm.
Pine, sand .... *Pinus clausa* (Engelm.) Sarg.
Pine, Scotch .... *Pinus sylvestris* L.
Pine, shortleaf .... *Pinus echinata* Mill.
Pine, slash .... *Pinus caribaea* More.
Pine, spruce .... *Pinus glabra* Walt.
Pine, sugar .... *Pinus lambertiana* Dougl.
Pine, Virginia .... *Pinus virginiana* Mill.
Pine, western white .... *Pinus monticola* D. Don.
Pine, whitebark .... *Pinus albicaulis* Engelm.
Piñon .... *Pinus edulis* Engelm.
Piñon, singleleaf .... *Pinus monophylla* Torr. & Fremont
Poisonwood .... *Metopium toxiferum* Krug & Urban
Poplar, white .... *Populus alba* L.
Poplar, yellow or tulip .... *Liriodendron tulipifera* L.
Redwood .... *Sequoia sempervirens* (Lamb.) Endl.
Sourwood .... *Oxydendrum arboreum* (L.) DC.
Spruce, bigcone .... *Pseudotsuga macrocarpa* (Torr.) Mayr
Spruce, black .... *Picea mariana* (Mill.) B. S. P.
Spruce, blue .... *Picea pungens* Engelm.
Spruce, Engelmann .... *Picea engelmannii* Engelm.
Spruce, Norway .... *Picea excelsa* Link
Spruce, red .... *Picea rubra* Link
Spruce, Sitka .... *Picea sitchensis* (Bong.) Carr.
Spruce, white .... *Picea glauca* (Moench) Voss
Sugarberry or southern hackberry *Celtis laevigata* Willd.
Sycamore .... *Platanus occidentalis* L.
Tamarack .... *Larix laricina* (DuRoi) Koch
Tamarind, wild .... *Lysiloma bahamensis* Benth.
Walnut, black .... *Juglans nigra* L.
Wattle, black .... *Acacia mollissima* Willd.
Willow .... *Salix* spp.
Yew, Pacific .... *Taxus brevifolia* Nutt.

BIBLIOGRAPHY

Aaltonen, V. T. 1925. Über den Aziditätsgrad (pH) des Waldbodens. *Comm. Inst. Forest. Finniae* **9**: 1–54.

——. 1926. On the space arrangement of trees and root competition. *Jour. Forestry* **24**: 627–644.

——. 1932. Über den Einfluss der Holzart auf den Boden. *Comm. Inst. Forest. Fenniae* **17**(5): 1–88.

Abbot, C. G. 1929. The sun. 433 pp. D. Appleton & Co., New York.

——. 1936. The influence of solar variability on weather. *Sci. Mo.* **43**: 108–121.

Abell, C. A. 1934. Influence of glaze storms upon hardwood forests in the Southern Appalachians. *Jour. Forestry* **32**: 35–37.

Adams, C. C. 1923. Notes on the relation of birds to Adirondack forest vegetation. *Roosevelt Wild Life Bul.* **1**(4): 487–519.

Adams, W. R. 1935. Studies in tolerance of New England forest trees: XII. Effect of thinning in plantations on some of the physical factors of the site and on the development of young northern white pine (*Pinus strobus* L.) and Scotch pine (*Pinus silvestris* L.). *Vt. Agr. Expt. Sta. Bul.* **390**. 156 pp.

Allard, H. A. 1932. Length of day in relation to the natural and artificial distribution of plants. *Ecology* **13**: 221–234.

Allen, W. E. 1929. The problem of significant variables in natural environments. *Ecology* **10**: 223–227.

Alway, F. J., and P. M. Harmer. 1927. Minnesota glacial soil studies: II. The forest floor on the Late Wisconsin Drift. *Soil Sci.* **23**: 57–70.

——, and J. Kittredge, Jr. 1933. The forest floor under stands of aspen and paper birch. *Soil Sci.* **35**: 307–312.

——, J. Kittredge, Jr., and W. J. Methley. 1933. Composition of the forest floor layers under different forest types on the same soil type. *Soil Sci.* **36**: 387–398.

——, M. A. Kline, and G. R. McDole. 1917. Some notes on the direct determination of the hygroscopic coefficient. *Jour. Agr. Research* **11**: 147–166.

——, and P. R. McMiller. 1933. Interrelationships of soil and forest cover on Star Island, Minnesota. *Soil Sci.* **36**: 281–294.

——, W. J. Methley, and O. R. Younge. 1933. Distribution of volatile matter, lime, and nitrogen among litter, duff, and leafmold under different forest types. *Soil Sci.* **36**: 399–407.

Anderson, D. B. 1936. Relative humidity or vapor pressure deficit. *Ecology* **17**: 277–282.

Angot, A. 1895. Régime des pluies de la peninsule Iberique. *Ann. Bur. Cent. Mét. France* **1**(1893), Sec. B, pp. 157–194.

Arthur, J. M. 1932. Red pigment production in apples by means of artificial light sources. *Boyce Thompson Inst. Contrib.* **4**: 1–18.

——. 1936. Some infra-red effects on green plants. *In* Biological Effects of Radiation, pp. 841–852. Ed. by B. M. Duggar. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

——, and W. D. Stewart. 1933. Transpiration of tobacco plants in relation to

radiant energy in the visible and infra-red. *Boyce Thompson Inst. Contrib.* **5**: 483–501.

——, and W. D. Stewart. 1935. Relative growth and dry-weight production of plant tissue under Mazda, neon, sodium, and mercury vapor lamps. *Boyce Thompson Inst. Contrib.* **7**: 119–130.

Asai, T. 1934. Uber das Vorkommen und die Bedeutung der Wurzelpilze in den Landpflanzen. *Japan Jour. Bot.* **7**: 107–150.

Ashe, W. W. 1915. A possible measure of light requirements of trees. *Soc. Amer. Foresters Proc.* **10**: 199–200.

——. 1926. Financial limitation in the employment of forest cover in protecting reservoirs. *U. S. Dept. Agr. Bul.* **1430.** 34 pp.

Atkins, W. R. G., and H. H. Poole. 1931. Photo-electric measurements of illumination in relation to plant distribution. Part 4. Changes in the color composition of daylight in the open and in shaded situations. *Roy. Dublin Soc. Sci. Proc.* **20**(N.S.): 13–48.

——, H. H. Poole, and F. A. Stanbury. 1937. The measurement of the intensity and the colour of the light in woods by means of emission and rectifier photo-electric cells. *Roy. Soc. London Proc., Ser. B.*, **121**(824): 427–450.

Auchter, E. C., and A. L. Schrader. 1929. Influence of shade on the behavior of apple trees. *Internatl. Cong. Plant Sci., Ithaca, N. Y., 1926, Proc.* **2**: 1056–1069. G. Banta Pub. Co., Menasha, Wis.

Auten, J. T. 1930. A soil study of the Mont Alto State Forest. *Penn. Dept. Forests and Waters Research Bul.* **4.** 64 pp.

——. 1933. Porosity and water absorption of forest soils. *Jour. Agr. Research* **46**: 997–1014.

——. 1934. Calcium and magnesium losses from cultivation of forest land. *Jour. Forestry* **32**: 419–424.

Bailey, R. W., C. L. Forsling, and R. J. Becraft. 1934. Floods and accelerated erosion in northern Utah. *U. S. Dept. Agr. Misc. Pub.* **196.** 21 pp.

Baker, F. S. 1929. Effect of excessively high temperatures on coniferous reproduction. *Jour. Forestry* **27**: 949–975.

——. 1934. Theory and practice of silviculture. 502 pp. McGraw-Hill Book Co., New York.

——, and C. F. Korstian. 1931. Suitability of brush lands in the intermountain region for the growth of natural or planted western yellow pine forests. *U. S. Dept. Agr. Tech. Bul.* **256.** 83 pp.

——, C. F. Korstian, and N. J. Fetherolf. 1921. Snowshoe rabbits and conifers in the Wasatch Mountains of Utah. *Ecology* **2**: 304–310.

Baldwin, H. I. 1934. Some physiological effects of girdling northern hardwoods. *Bul. Torrey Bot. Club* **61**: 249–257.

——. 1942. Forest tree seed of the north temperate regions with special reference to North America. 240 pp. Chronica Botanica Co., Waltham, Mass.

Barr, P. M. 1930. The effect of soil moisture on the establishment of spruce reproduction in British Columbia. *Yale Univ. School Forestry Bul.* **26.** 78 pp.

Bates, C. G. 1911. Windbreaks, their influence and value. *U. S. Dept. Agr., Forest Serv. Bul.* **86.** 100 pp.

——. 1918. Concerning site. *Jour. Forestry* **16**: 383–388.

——. 1923. The transect of a mountain valley. *Ecology* **4**: 54–62.

——. 1924. Forest types in the central Rocky Mountains as affected by climate and soil. *U. S. Dept. Agr. Bul.* **1233.** 152 pp.

——. 1925. The relative light requirements of some coniferous seedlings. *Jour. Forestry* **23:** 869–879.

——. 1931. A new principle in seed collecting for Norway pine. *Jour. Forestry* **29:** 661–678.

——, and A. J. Henry. 1928. Forest and stream-flow experiments at Wagon Wheel Gap, Colo. *U. S. Mo. Weather Rev. Sup.* **30.** 79 pp.

——, H. C. Hilton, and T. Kreuger. 1929. Experiments in the silvicultural control of natural reproduction of lodgepole pine in the central Rocky Mountains. *Jour. Agr. Research* **38:** 229–243.

——, and J. Roeser, Jr. 1924. Relative resistance of tree seedlings to excessive heat. *U. S. Dept. Agr. Bul.* **1263.** 16 pp.

——, and J. Roeser, Jr. 1928. Light intensities required for growth of coniferous seedlings. *Amer. Jour. Bot.* **15:** 185–194.

——, and R. Zon. 1922. Research methods in the study of forest environment. *U. S. Dept. Agr. Bul.* **1059.** 208 pp.

Baumann, A. 1909. Untersuchungen über die Humussäuren. *Mitt. K. Bayer. Moorkulturanst.* **3:** 52–123.

Baver, L. D. 1934. A classification of soil structure and its relation to the main soil groups. *Amer. Soil Survey Assoc. Rpt.* **15:** 107–109.

Baxter, D. V. 1943. Pathology in forest practice. 618 pp. John Wiley & Sons, New York.

Beall, H. W. 1934. The penetration of rainfall through hardwood and softwood forest canopy. *Ecology* **15:** 412–415.

Benecke, W., and L. Jost. 1923, 1924. Pflanzenphysiologie. (4 Aufl. von Jost, Verlesungen über Pflanzenphysiologie) 2 Bd. 441 + 447 s. Gustav Fischer, Jena.

Benedict, H. M. 1912. Senility in meristematic tissue. *Science N. S.* **35:** 421–422.

Bennett, H. H., and W. R. Chapline. 1928. Soil erosion a national menace. *U. S. Dept. Agr. Circ.* **33.** 36 pp.

Bergman, H. F., and H. Stallard. 1916. The development of climax formations in northern Minnesota. *Minn. Bot. Studies* **4:** 333–378.

Betts, N. DeW. 1916. Notes on forest cover and snow retention on the east slope of the front range in Colorado. *Soc. Amer. Foresters Proc.* **11:** 27–32.

Biswell, H. H. 1935. Effects of environment upon the root habits of certain deciduous forest trees. *Bot. Gaz.* **96:** 676–708.

Blackman, F. F. 1905. Optima and limiting factors. *Ann. Bot. [London]* **19:** 281–295.

——, and G. L. C. Matthaei. 1905. Experimental researches in vegetable assimilation and respiration. IV. A quantitative study of carbon-dioxide assimilation and leaf-temperature in natural illumination. *Proc. Royal Soc. London, Ser. B,* **76:** 402–460.

Bodman, G. B., and N. E. Edlefsen. 1934. The soil moisture system. *Soil Sci.* **38:** 425–444.

Bolas, B. D. 1926. The control of atmospheric humidity in a closed system. *New Phytol.* **25:** 119–126.

Bonnier, G. 1920. Nouvelles observations sur les cultures expérimentales a diverses altitudes et cultures par semis. *Rev. Gén. Bot.* **32:** 305–326.

BORNEBUSCH, C. H. 1930. The fauna of forest soil. *Forstl. Forsgsv. Danmark* **11**: 1–224.

——, and S. O. HEIBERG. 1936. Proposal to the Third International Congress of Soil Science, Oxford, England, 1935, for the nomenclature of forest humus layers. *Third Internatl. Cong. Soil Sci., Oxford, 1935, Trans.* **3**: 260–261.

BORTHWICK, A. W. 1934. Some aspects of forest biology. *Scot. Forestry Jour.* **48**: 105–120.

BOUYOUCOS, G. J. 1927. The hydrometer as a new and rapid method for determining the colloidal content of soils. *Soil Sci.* **23**: 319–330.

——. 1928. The hydrometer method for making a very detailed mechanical analysis of soils. *Soil Sci.* **26**: 233–238.

——. 1928. Making mechanical analyses of soils in fifteen minutes. *Soil Sci.* **25**: 473–480.

——. 1929. The ultimate natural structure of soil. *Soil Sci.* **28**: 27–37.

——. 1930. A comparison of the hydrometer method and the pipette method for making mechanical analysis of soils, with new directions. *Jour. Amer. Soc. Agron.* **23**: 747–751.

BOWMAN, I. 1914. Forest physiography. 759 pp. John Wiley & Sons, New York.

BOYCE, J. S. 1938. Forest pathology. 600 pp. McGraw-Hill Book Co., New York.

BRACKETT, F. S. 1936. Measurement and application of visible and near-visible radiation. *In* Biological Effects of Radiation, pp. 123–209. Ed. by B. M. DUGGAR. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

BRAUN-BLANQUET, J. 1932. Plant sociology: the study of the plant communities. (Pflanzensoziologie.) Trans., rev., and ed. by G. D. FULLER and H. S. CONARD. 439 pp. McGraw-Hill Book Co., New York.

BRAY, W. L. 1910. The mistletoe pest in the Southwest. *U. S. Dept. Agr., Bur. Plant Ind. Bul.* **166**. 39 pp.

BREAZEALE, J. F. 1930. Maintenance of moisture-equilibrium and nutrition of plants at and below the wilting percentage. *Ariz. Agr. Expt. Sta. Tech. Bul.* **29**: 139–177.

——. 1934. Fundamental concepts in plant research. *Ariz. Agr. Expt. Sta. Bul.* **147**. 84 pp.

——, and F. J. CRIDER. 1934. Plant association and survival, and the build-up of moisture in semi-arid soils. *Ariz. Agr. Expt. Sta. Tech. Bul.* **53**: 95–123.

BREWER, W. H. 1874. The woodlands and forest systems of the United States. 5 pp. *In* Statistical atlas of the United States based on the results of the 9th census, 1870. By F. A. WALKER. J. Bien, Lith., New York.

——. 1890. Report of the committee on the relation of forestry to the public health. *Conn. State Board of Public Health.* 13 pp. New Haven.

BREWSTER, D. R. 1918. Relation between height growth of larch seedlings and weather conditions. *Jour. Forestry* **16**: 861–870.

BRIGGS, L. J., and H. L. SHANTZ. 1912. The wilting coefficient and its indirect determination. *Bot. Gaz.* **53**: 20–37.

——, and H. L. SHANTZ. 1912. The wilting coefficient for different plants and its indirect determination. *U. S. Dept. Agr., Bur. Plant Ind. Bul.* **230**. 83 pp.

BROCKMANN-JEROSCH, H. 1919. Baumgrenze und Klimacharakter. *Beitr. Geobot. Landesaufn.* **6**. 255 s. Rascher & Cie., Zürich.

Brown, H. T., and F. Escombe. 1905. Researches on some of the physiological processes of green leaves, with special reference to the interchange of energy between the leaf and its surroundings. *Proc. Roy. Soc. London, Ser. B.* **76**: 29–111.

Brown, J., and J. Nisbet. 1894. The forester: a practical treatise on the planting and tending of forest trees and the general management of woodland estates. 2 vols. 629 + 545 pp. Wm. Blackwood & Sons, London.

Brown, W. H. 1918. The theory of limiting factors. *Philippine Jour. Sci.; Bot.* **13**: 345–350.

Bruce, D., and F. X. Schumacher. 1942. Forest mensuration. 2nd Ed. 425 pp. McGraw-Hill Book Co., New York.

Brückner, E. 1890. Klimaschwankungen seit 1700 nebst Bemerkungen über die Klimaschwankungen der Diluvialzeit. 324 s. E. Hölzel, Wien.

——. 1905. Die Bilanz des Kreislaufs des Wassers auf der Erde. *Geogr. Ztschr.* **11**: 436–445.

Bühler, A. 1910. Untersuchungen über die Bildung von Waldhumus. *Mitt. Württemb. Forstl. Versuchsanst.* **2**. 70 s. E. Ulmer, Stuttgart.

——. 1918, 1927. Der Waldbau nach wissenschaftlicher Forschung und praktischer Erfahrung. 1 Bd. (1918.) 662 s. 2 Bd. 2 Aufl. (1927.) 679 s. E. Ulmer, Stuttgart.

Burger, H. 1922. Physikalische Eigenschaften der Wald- und Freilandböden. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **13**: 1–221.

——. 1923. Physikalische Eigenschaften von Wald- und Freilandböden. II. Einfluss der Durchforstungsart auf die physikalischen Eigenschaften der Waldböden. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **14**: 201–250.

——. 1925. Die Transpiration unserer Waldbäume. *Ztschr. Forst. u. Jagdw.* **57**: 473–482.

Burges, A. 1936. On the significance of mycorrhizae. *New Phytol.* **35**(2): 117–131.

Burkholder, P. R. 1936. The rôle of light in the life of plants. *Bot. Rev.* **2**: 1–52, 97–172.

Burns, G. P. 1916. Studies in tolerance of New England forest trees. III. Discontinuous light in forests. *Vt. Agr. Expt. Sta. Bul.* **193**. 23 pp.

——. 1923. Measurement of solar radiant energy in plant habitats. *Ecology* **4**: 189–195.

——. 1923. Studies in tolerance of New England forest trees. IV. Minimum light requirement referred to a definite standard. *Vt. Agr. Expt. Sta. Bul.* **235**. 32 pp.

——. 1927. Studies in tolerance of New England forest trees. VII. Leaf efficiency in thrifty and stunted white pine seedlings. *Vt. Agr. Expt. Sta. Bul.* **267**. 27 pp.

Burns, G. R. 1933. Photosynthesis in various portions of the spectrum. *Plant Physiol.* **8**: 247–262.

——. 1935. Long and short wave-length limits of photosynthesis. *Plant Physiol.* **9**: 645–652.

Burt, F. A. 1927. Soil mineralogy. 82 pp. D. Van Nostrand Co., New York.

Büsgen, M., and E. Münch. 1931. The structure and life of forest trees (Bau und Leben unserer Waldbäume). Eng. trans. by T. Thompson. 436 pp. John Wiley & Sons, New York.

CAHALANE, V. H. 1928. A preliminary wild life and forest survey of southwestern Cattaraugus County, New York. *Roosevelt Wild Life Bul.* **5**(1): 9–144.

CAIN, S. A. 1931. Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee: I. Soil reaction and plant distribution. *Bot. Gaz.* **91**: 22–41.

——. 1944. Foundations of plant geography. 556 pp. Harper and Bros., New York.

CAJANDER, A. K. 1909, 1913. Ueber Waldtypen. *Acta Forest. Fennica* **1**: 1–175.

——. 1926. The theory of forest types. *Acta Forest. Fennica* **29**(3): 1–108.

——. 1930. Wesen und Bedeutung der Waldtypen. *Silva Fennica* **15**: 1–66.

CALDWELL, J. S. 1913. The relation of environmental conditions to the phenomenon of permanent wilting in plants. *Physiol. Researches* **1**: 1–56.

CAMERON, F. K. 1911. The soil solution: The nutrient medium for plant growth. 136 pp. The Chemical Pub. Co., Easton, Pa.

CANNON, W. A. 1911. The root habits of desert plants. *Carnegie Inst. Wash. Pub.* **131**. 96 pp.

——. 1913. Some relations between root characters and ground-water and species distribution. *Science N. S.* **37**: 420–423.

——. 1916. Distribution of the cacti with especial reference to the rôle played by the root response to soil temperature and soil moisture. *Amer. Nat.* **50**: 435–442.

——. 1917. Relation of the rate of root growth in seedlings of *Prosopis velutina* to the temperature of the soil. *Plant World* **20**: 320–333.

——. 1918. The evaluation of the soil temperature factor in root growth. *Plant World* **21**: 64–67.

——. 1922. Root-growth in relation to a deficiency of oxygen or an excess of carbon dioxide in the soil. *Carnegie Inst. Wash. Yearbook* **20**: 48–51.

——. 1923. The influence of the temperature of the soil on the relation of roots to oxygen. *Science N. S.* **58**: 331–332.

——. 1924. Experimental investigations on roots. *Carnegie Inst. Wash. Yearbook* **22**: 56–62.

——. 1925. Experimental studies on roots. *Carnegie Inst. Wash. Yearbook* **24**: 289–298.

——, and E. E. FREE. 1917. The ecological significance of soil aeration. *Science N. S.* **45**: 178–180.

——, and E. E. FREE. 1925. Physiological features of roots, with especial reference to the relation of roots to aeration of the soil. *Carnegie Inst. Wash. Pub.* **368**. 168 pp.

CARD, F. W. 1897. Windbreaks. *Nebr. Agr. Expt. Sta. Bul.* **48**. 96 pp.

CARPENTER, L. G. 1901. Forests and snow. *Colo. Agr. Expt. Sta. Bul.* **55**. 10 pp.

CHAPMAN, H. H. 1926. Factors determining natural reproduction of longleaf pine in LaSalle Parish, Louisiana. *Yale Univ. School Forestry Bul.* **16**. 44 pp.

CHASE, H. 1913. Game protection and propagation in America. 238 pp. J. B. Lippincott, Philadelphia.

CHEYNEY, E. G. 1942. American silvics and silviculture. 472 pp. Univ. Minn. Press, Minneapolis.

CHURCH, J. E., JR. 1912. The conservation of snow: its dependence on mountains and forests. *Internatl. Irrig. Cong. Bul.* **1**: No. 6. 52 pp.

CHURCH, J. E. 1913. Das Verhältnis des Waldes und des Gebirges zur Erhaltung des Schnees. *Met. Ztschr.* **30**(1): 1–10.

CIESLAR, A. 1904. Einiges über die Rolle des Lichtes im Walde. *Mitt. Forstl. Versuchsw. Österr.* **30**: 1–105.

——. 1907. Die Bedeutung klimatischer Varietäten unserer Holzarten für den Waldbau. *Centbl. Gesam. Forstw.* **33**: 49–62.

——. 1923. Untersuchungen über die wirtschaftliche Bedeutung der Herkunft des Saatgutes der Stieleiche. *Centbl. Gesam. Forstw.* **49**: 97–149.

CLEMENT, G. E., and W. MUNRO. 1917. Control of the gipsy moth by forest management: Part I. The gipsy moth in woods. By G. E. CLEMENT. Part II. Management of typical woodlots infested with the gipsy moth in the white-pine region. By W. MUNRO. *U. S. Dept. Agr. Bul.* **484.** 54 pp.

CLEMENTS, E. S. 1905. The relation of leaf structure to physical factors. *Amer. Micros. Soc. Trans.* **26**: 19–102.

CLEMENTS, F. E. 1904. Studies in the vegetation of the state. III: The development and structure of vegetation. *Nebr. Univ., Rpt. Bot. Survey Nebr.* **7.** 175 pp.

——. 1905. Research methods in ecology. 334 pp. Univ. Pub. Co., Lincoln, Neb.

——. 1909. Plant formations and forest types. *Soc. Amer. Foresters Proc.* **4**: 50–63.

——. 1910. The life history of lodgepole burn forests. *U. S. Dept. Agr., Forest Serv. Bul.* **79.** 56 pp.

——. 1916. Plant succession, an analysis of the development of vegetation. *Carnegie Inst. Wash. Pub.* **242.** 512 pp.

——. 1920. Plant indicators: the relation of plant communities to process and practice. *Carnegie Inst. Wash. Pub.* **290.** 388 pp.

——. 1921. Aeration and air content: the rôle of oxygen in root activity. *Carnegie Inst. Wash. Pub.* **315.** 183 pp.

——. 1928. Plant succession and indicators. 453 pp. H. W. Wilson, New York.

——. 1936. Nature and structure of the climax. *Jour. Ecology* **24**: 252–284.

——, and E. V. MARTIN. 1934. Effects of soil temperature on transpiration in *Helianthus annuus*. *Plant Physiol.* **9**: 619–630.

——, J. E. WEAVER, and H. C. HANSON. 1929. Plant competition: an analysis of community functions. *Carnegie Inst. Wash. Pub.* **398.** 340 pp.

CLEPPER, H. E. 1931. The deer problem in the forests of Pennsylvania. *Penn. Dept. Forests and Waters Bul.* **50.** 45 pp.

CLUM, H. H. 1926. The effect of transpiration and environmental factors on leaf temperatures. *Amer. Jour. Bot.* **13**: 194–216, 217–230.

COILE, T. S. 1933. Soil reaction and forest types in the Duke Forest. *Ecology* **14**: 323–333.

——. 1935. Relation of site index for shortleaf pine to certain physical properties of the soil. *Jour. Forestry* **33**: 726–730.

——. 1936. The effect of rainfall and temperature on the annual radial growth of pine in the southern United States. *Ecological Monog.* **6**: 533–562.

——. 1936. Soil samplers. *Soil Sci.* **42**: 139–142.

——. 1937. Distribution of forest tree roots in North Carolina Piedmont soils. *Jour. Forestry* **35**: 247–257.

——. 1940. Soil changes associated with loblolly pine succession on abandoned

agricultural land of the Piedmont Plateau. *Duke Univ. School Forestry Bul.* **5.** 85 pp.

COTTA, H. 1804. Systematische Anleitung zur Taxation der Waldungen. 2 Bd., 192 + 216 s. Berlin.

COULTER, J. M., C. R. BARNES, and H. C. COWLES. 1930–1931. A textbook of botany for colleges and universities. Vol. 1. Morphology. (Rev. by J. M. COULTER.) 310 pp. 1930. Vol. 2. Physiology. (Rev. by C. A. SHULL.) 307 pp. 1930. Vol. 3. Ecology. (Rev. by G. D. FULLER.) 499 pp. 1931. American Book Co., New York.

COWLES, H. C. 1901. The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. *Bot. Gaz.* **31**: 73–108, 145–182.

CRAIB, I. J. 1929. Some aspects of soil moisture in the forest. *Yale Univ. School Forestry Bul.* **25.** 62 pp.

——. 1934. The place of thinning in wattle silviculture and its bearing on the management of exotic conifers. *Ztschr. Weltforstw.* **1**: 77–108.

CROCKER, W. 1916. Mechanics of dormancy in seeds. *Amer. Jour. Bot.* **3**: 99–120.

——. 1918. Law of the minimum — a review of Hooker's work. *Bot. Gaz.* **65**: 287–288.

CROMER, D. A. N. 1935. The significance of the mycorrhiza of *Pinus radiata*. *Aust. Commonwealth Forestry Bur. Bul.* **16.** 19 pp.

CURTIS, H. A. 1932. General survey of the sources and utilization of fixed nitrogen. *In* Fixed Nitrogen, pp 11–22. The Chemical Catalog Co., New York.

CURTIS, O. F. 1936. Comparative effects of altering leaf temperatures and air humidities on vapor pressure gradients. *Plant Physiol.* **11**: 595–603.

DARROW, K. K. 1936. Photons and electrons. *In* Biological Effects of Radiation. pp. 1–42. Ed. by B. M. DUGGAR. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

DARWIN, C. R. 1881. The power of movement in plants. 592 pp. D. Appleton & Co., New York.

DAVIS, A. R., and D. R. HOAGLAND. 1928. Further experiments on the growth of plants in a controlled environment. I. The relation of light intensity and exposure time to yield. II. The interrelationship of temperature and light. *Amer. Jour. Bot.* **15**: 624.

DAVIS, R. O. E., and H. H. BENNETT. 1927. Grouping of soils on the basis of mechanical analysis. *U. S. Dept. Agr. Circ.* **419.** 14 pp.

DAWSON, J. 1885. The propagation of trees and shrubs from seed. *Mass. Hort. Soc. Trans. 1885,* Pt. 1, pp. 145–164.

DAXER, H. 1934. Über die Assimilationsökologie der Waldbodenflora. *Jahrb. Wiss. Bot.* **80**: 363–420.

DEEN, J. L. 1933. Some aspects of an early expression of dominance in white pine (*Pinus strobus* L.). *Yale Univ. School Forestry Bul.* **36.** 34 pp.

DENGLER, A. 1908. Das Wachstum von Kiefern aus einheimischem und nordischem Saatgut in der Oberförsterei Eberswalde. *Ztschr. Forst u. Jagdw.* **40**: 137–152, 206–219.

——. 1935. Waldbau auf ökologischer Grundlage. 2 Aufl. 556 s. J. Springer, Berlin.

DEUBER, C. G. 1936. Effects on trees of an illuminating gas in the soil. *Plant Physiol.* **11**: 401–412.

DEVRIES, H. 1901, 1903. Die Mutationstheorie. 2 Bd. 648 + 752 pp. Vert. & Comp., Leipzig.

DEXTER, S. T. 1933. Decreasing hardiness of winter wheat in relation to photosynthesis, defoliation, and winter injury. *Plant Physiol.* **8**: 297–304.

——. 1933. Effect of several environmental factors on the hardening of plants. *Plant Physiol.* **8**: 123–139.

DICE, L. R. 1931. The relation of mammalian distribution to vegetation types. *Sci. Mo.* **33**: 312–317.

DITTMAR, H. J. A. 1921. Der Waldbau; ein Leitfaden für den Unterricht und die Praxis, ein Handbuch für den Privatwaldbesitzer. 285 s. J. Neumann, Neudamm.

DOAK, K. D. 1934. Fungi that produce ectotrophic mycorrhizae of conifers. *Phytopath.* **24**: 7, abs.

DOANE, R. W., E. C. VAN DYKE, W. J. CHAMBERLAIN, and H. E. BURKE. 1936. Forest insects. 463 pp. McGraw-Hill Book Co., New York.

DOKUCHAEV, V. V. 1879. (Kartographie der Russischen Böden) (German trans. of Russian text). *Zemledieliia i selskoĭ promyshlennosti, Department.* 114 pp.

DOLE, E. J. 1924. Studies on the effects of air temperature and relative humidity on the transpiration of *Pinus strobus*. *Vt. Agr. Expt. Sta. Bul.* **238**. 39 pp.

DOUGLASS, A. E. 1928. Climatic cycles and tree-growth. *Carnegie Inst. Wash. Pub.* **289**, Vol. II. 166 pp.

DRUDE, O. 1890. Über die Principien in der Unterscheidung von Vegetationsformationen, erläutert an der centraleuropäischen Flora. *Bot. Jahrb. System. Pflanzengeschichte Pflanzengeogr.* **11**: 21–51.

——. 1896. Deutschlands Pflanzengeographie. Bd. 1. 502 s. J. Engelhorn, Stuttgart.

——. 1913. Die Ökologie der Pflanzen. 308 pp. Friedr. Vieweg & Sohn, Braunschweig.

DÜESBERG, R. M. J. 1910. Der Wald als Erzieher. 201 pp. Paul Parey, Berlin.

DUGGAR, B. M., and A. R. DAVIS. 1916. Studies in the physiology of the fungi. *Ann. Missouri Bot. Gard.* **3**: 413–437.

——, and F. C. STEWART. 1909. Fungous diseases of plants. 508 pp. Ginn & Co., Boston.

——, et al. 1936. Biological effects of radiation. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

DUMOND, F. L. 1922. Branch orders and tolerance. *Jour. Forestry* **20**: 448–462.

DUMONT, J. 1909. Les enduits de revêtement des particules terreuses. *Compt. Rend.* **149**: 1087–1089.

DUNCKELMAN, B. 1881. Kiefern-Unterbaubetrieb. *Ztschr. Forst u. Jagdw.* **13**: 1–7.

DUNNING, D. 1928. A tree classification for the selection forests of the Sierra Nevada. *Jour. Agr. Research* **36**: 755–771.

DU RIETZ, G. E. 1929. The fundamental units of vegetation. *Internatl. Cong. Plant Sci. Ithaca, N. Y., 1926, Proc.* **1**: 623–627.

——. 1930. Vegetationsforschung auf soziationsanalytischer Grundlage. *Handb. Biol. Arbeitsmeth. Abderhalden* XI. **5**: 293–480.

EBERMAYER, E. 1873. Die physikalischen Einwirkung des Waldes auf Luft und

Boden und seine klimatologische und hygienische Bedeutung, begründet durch die Beobachtungen der forstl.-meteorolog. Station im königreich Bayern. 253 s. C. Krebs, Aschaffenburg.

EBERMAYER, E. W. F. 1876. Die gesammte Lehre der Waldstreu mit Rücksicht auf die chemische Statik des Waldbaues. 300 s. J. Springer, Berlin.

——. 1890. Hygienische Bedeutung des Waldes begründet durch exacte Untersuchungen der Waldluft und des Waldbodens. 19 s. Landwirthschafts-Gesellschaft, Wien.

EHRENBERG, P. 1922. Die Bodenkolloide; eine Erzanzüng für die üblichen Lehrbücher der Bodenkunde, Düngerlehre, und Ackerbaulehre. 717 s. T. Steinkopff, Dresden und Leipzig.

ENGLER, A. 1903. Untersuchungen über das Wurzelwachstum der Holzarten. *Mitt. Schweiz. Centralanst. Forstl. Versuchw.* 7: 247–317.

——. 1905. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **8**: 81–236.

——. 1913. Einfluss der Provenienz des Samens auf die Eigenschaften der forstlichen Holzgewächse. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **10**: 189–196.

——. 1919. Untersuchungen über den Einfluss des Waldes auf den Stand der Gewässer. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **12**: 1–626.

——. 1924. Heliotropismus und Geotropismus der Bäume und deren waldbauliche Bedeutung. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **13**: 225–283.

FABRICIUS, L. 1927. Der Einfluss der Wurzelwettbewerbs des Schirmstandes auf die Entwicklung des Jungwuchses. *Forstw. Centbl.* **49**: 329–345.

——. 1929. Neue Versuche zur Feststellung des Einflusses von Wurzelwettbewerb und Lichtentzug des Schirmstandes auf den Jungwuchs. *Forstw. Centbl.* **51**: 477–506.

FALCK, R. 1923. Erweiterte Denkschrift über die Bedeutung der Fadenpilze für die Nutzbarmachung der Abfallstoffe zur Baumernährung im Walde und über die Möglichkeit einer nachträglichen pilzlichen Aufschiessung des Trockentorfs. *Mykol. Untersuch., Ber.* **2**: 38–72.

FALLOU, F. A. 1862. Pedologie oder allgemeine und besondere Bodenkunde. Dresden.

FEHER, D. 1933. Untersuchungen über die Mikrobiologie des Waldbodens. 272 s. J. Springer, Berlin.

FERNALD, M. L. 1919. Lithological factors limiting the ranges of *Pinus banksiana* and *Thuja occidentalis*. *Rhodora* **21**: 41–67.

FERNOW, B. E. 1890. Forests and floods. *Garden and Forest* **3**: 9–10.

——. 1902. Economics of forestry. 5th Ed. 520 pp. T. Y. Crowell Co., New York.

——. 1905. Forest terminology. *Forestry Quart.* **3**: 255–268.

——, M. W. HARRINGTON, C. ABBE, and G. E. CURTISS. 1893. Forest influences. *U. S. Dept. Agr., Forestry Div. Bul.* 7. 197 pp.

FISHER, R. T. 1928. Soil changes and silviculture on the Harvard Forest. *Ecology* **9**: 6–11.

FLURY, P. 1932. Untersuchungen über den Lichtungsbetrieb an Bäumen und

Beständen. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **17**: 245–297. (French résumé), p. 298.

FORSLING, C. L. 1931. A study of the influence of herbaceous plant cover on surface run-off and soil erosion in relation to grazing on the Wasatch Plateau in Utah. *U. S. Dept. Agr. Tech. Bul.* **220.** 72 pp.

FOWLE, F. E. 1933. Smithsonian physical tables. 8th Ed. *Smithsn. Misc. Collect.* **88**: 1–682. Pub. 3171.

FRANK, B. 1885. Ueber die auf Wurzelsymbiose beruhende Ernahrung gewisser Bäume durch unterirdische Pilze. *Ber. Deut. Bot. Gesell.* **3**: 128–145.

FRANK, B. 1889. Ueber den experimentellen Nachweis der Assimilation freien Stickstoffs durch erdbodenbewohnende Algen. *Ber. Deut. Bot. Gesell.* **7**: 34–42.

FRANK, E. 1927. Über Bodenazidität im Walde. 155 s. H. M. Muth, Freiburg.

FRICKE, K. 1904. "Licht- und Schattenholzarten," ein wissenschaftlich nicht begründetes Dogma. *Centbl. Gesam. Forstw.* **30**: 315–325.

FRITZ, E., and J. L. AVERILL. 1924. Discontinuous growth rings in California redwood. *Jour. Forestry* **22**(6): 31–38.

FRÖDIN, J. 1920. La limite forestière alpine et la température de l'air. *Bot. Notiser* **1920**: 167–176.

FROTHINGHAM, E. H. 1918. Height growth as a key to site. *Jour. Forestry* **16**: 754–760.

FULLER, G. D. 1920. Topographic relief as a factor in plant succession. *Ill. State Acad. Sci. Trans.* **13**: 243–247.

FÜRST, H. 1893. The protection of woodlands against dangers arising from organic and inorganic causes. (Eng. trans. by JOHN NISBET.) 252 pp. David Douglas, Edinburgh.

GABRIELSON, I. N., and E. E. HORN. 1930. Porcupine control in the western United States. *U. S. Dept. Agr. Leaflet* **60.** 8 pp.

GAIL, F. W. 1921. Factors controlling the distribution of Douglas fir in semi-arid regions of the northwest. *Ecology* **2**: 281–291.

——. 1926. Osmotic pressure of cell sap and its possible relation to winter killing and leaf fall. *Bot. Gaz.* **81**: 434–445.

GARNER, W. W. 1931. Duration of the flowerless condition of some plants in response to unfavorable lengths of day. *Jour. Agr. Research* **43**: 439–443.

——. 1933. Comparative responses of long-day and short-day plants to relative length of day and night. *Plant Physiol.* **8**: 347–356.

——, and H. A. ALLARD. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Jour. Agr. Research* **18**: 553–606.

——, and H. A. ALLARD. 1923. Further studies in photoperiodism, the response of the plant to relative length of day and night. *Jour. Agr. Research* **23**: 871–920.

——, and H. A. ALLARD. 1931. Effect of abnormally long and short alternations of light and darkness on growth and development of plants. *Jour. Agr. Research* **42**: 629–651.

GAST, P. R. 1930. A thermoelectric radiometer for silvical research: with preliminary results on the relation of insolation to the growth of white pine. *Harvard Forest Bul.* **14.** 76 pp.

GATES, F. C. 1911. Light as a factor inducing plant succession. *Mich. Acad. Sci. Ann. Rpt.* **13**: 201–202.

GAYER, K. 1886. Der Gemischte Wald; seine Begründung und Pflege, insbesondere durch Horst- und Gruppenwirtschaft. 168 pp. Berlin.

——. 1898. Der Waldbau. 4 Aufl. 626 s. P. Parey, Berlin.

GEHRHART, C. 1929. Schnellwuchsbetrieb in Jütland. *Forstl. Wochenschrift Silva* **17**: 297–301, 305–307.

GEIGER, R. 1927. Das Klima der Bodennahen Luftschicht. 246 s. F. Vieweg u. Sohn, Braunschweig.

GERHARDT, P., J. ABROMEIT, P. BOCK, and A. JENTZSCH. 1900. Handbuch des deutschen Dünenbaues. Im Auftrage des Kgl. Preuss. Ministeriums der offentlichen Arbeiten. 656 pp. Paul Parey, Berlin.

GISBORNE, H. T. 1926. Lightning and forest fires in the northern Rocky Mountain region. *U. S. Mo. Weather Rev.* **54**: 281–286.

GLEASON, H. A. 1920. Some applications of the quadrat method. *Bul. Torrey Bot. Club* **47**: 21–33.

GLENN, L. C. 1911. Denudation and erosion in the southern Appalachian region and the Monongahela Basin. *U. S. Geol. Survey, Prof. Paper* **72**. 137 pp.

GLINKA, K. D. 1927. The great soil groups of the world and their development (Eng. trans. by C. F. MARBUT.) 150 pp. Edwards Brothers, Ann Arbor.

GOLDSMITH, G. W. 1923. Some field instruments and their application. *Nebr. Univ., Studies* **23**: 201–264.

GOODWIN, W. N., JR. 1932. The photronic illumination meter. *Illum. Engin. Soc. Trans.* **27**: 828–835.

GRÄBNER, P. 1901. Wie bilden sich Wald, Wiese, und Moor. *Gartenflora* **50**: 567–573. (Referate im *Bot. Centbl.* **89**: 140. 1902.)

GRAHAM, S. A. 1928. The influence of small mammals and other factors upon the larch sawfly survival. *Jour. Econ. Ent.* **21**: 301–310.

——. 1929. Principles of forest entomology. 339 pp. McGraw-Hill Book Co., New York.

GRASOVSKY, A. 1929. Some aspects of light in the forest. *Yale Univ. School Forestry Bul.* **23**. 53 pp.

GRAVES, H. S. 1899. Practical forestry in the Adirondacks. *U. S. Dept. Agr., Div. Forestry Bul.* **26**. 77 pp.

——. 1911. Principles of handling woodlands. 325 pp. John Wiley & Sons, New York.

——, and E. A. ZIEGLER. 1910. The woodsman's handbook. (Rev. Ed.) *U. S. Dept. Agr., Forest Service Bul.* **36**. 208 pp.

GREBE, C. 1886. Gebirgskunde, Bodenkunde und Klimalehre in ihrer Anwendung auf Forstwirtschaft. 316 s. P. Parey, Berlin.

GREELEY, W. B. 1913. Classification of forest types. *Soc. Amer. Foresters Proc.* **8**: 76–78.

GRIFFIN, A. A. 1918. Influence of forests upon the melting of snow in the Cascade range. *U. S. Mo. Weather Rev.* **46**: 324–327.

GRIFFITH, B. G., E. W. HARTWELL, and T. E. SHAW. 1930. The evolution of soils as affected by the old field white pine-mixed hardwood succession in central New England. *Harvard Forest Bul.* **15**. 82 pp.

GRIFFON, E. 1900. L'assimilation chlorophyllienne dans la lumière solaire qui a traversé des feuilles. *Rev. Gén. Bot.* **12**: 209–223, 272–288.

GRISEBACH, A. 1838. Ueber den Einfluss des Climas auf die Begränzung der natürlichen Floren. *Linnaea* **12**: 159–200.

GUT, R. C. 1929. Le gaz carbonique dans l'atmosphère forestière. *Bich. Ztschr. Schweiz. Forstvereins No.* **3**. 112 pp.

HAASIS, F. W. 1921. Relations between soil type and root form of western yellow pine seedlings. *Ecology* **2**: 292–303.

——. 1923. Frost heaving of western yellow pine seedlings. *Ecology* **4**: 378–390.

——. 1934. Diametral changes in tree trunks. *Carnegie Inst. Wash. Pub.* **450**. 103 pp.

HAIG, I. T. 1929. Colloidal content and related soil factors as indicators of site quality. *Yale Univ. School Forestry Bul.* **24**. 33 pp.

——. 1936. Factors controlling initial establishment of western white pine and associated species. *Yale Univ. School Forestry Bul.* **41**. 149 pp.

HALSTED, B. D., and S. A. WAKSMAN. 1917. The influence of soil temperature upon seedling corn. *Soil Sci.* **3**: 393–398.

HAMBERG, H. E. 1885–1889. Om skogarnes inflytande på Sveriges klimat. (De l'influence des forêts sur le climat de la Suède.) 3 pts. 2 maps. Stockholm. *From* Domän-styrelsens underdåniga berättelse rorande skogsväsendet Bihang, 1884–87.

HANN, J. 1903. Handbook of climatology. (Eng. trans. by R. DEC. WARD.) 437 pp. The Macmillan Co., New York.

HARDER, R. 1921. Kritische Versuche zu Blackmans Theorie der 'begrenzenden Faktoren' bei der Kohlensäureassimiliation. *Jahrb. Wiss. Bot.* **60**: 531–571.

HARLOW, W. M., and E. S. HARRAR. 1941. Textbook of dendrology: Covering the important forest trees of the United States and Canada. 2nd Ed. 542 pp. McGraw-Hill Book Co., New York.

HARMER, P. M. 1926. Minnesota glacial soil studies. III. Density of the surface foot in forest and prairie on the Late Wisconsin Drift. *Soil Sci.* **23**: 73–80.

HARRISON, W. H., and P. A. SUBRAMANIA AIYER. 1914. The gases of swamp rice soils. II. Their utilization for the aeration of the roots of the crop. *Mem. Dept. Agr. India, Chem. Ser.* **4**: 1–17.

HARTIG, R. 1886. Ueber symbiotische Erscheinungen im Pflanzen Leben. *Bot. Centbl.* **25**: 350–352.

——. 1889. Lehrbuch der Baumkrankheiten. 2 Aufl. 291 s. J. Springer, Berlin.

——. 1891. Lehrbuch der Anatomie und Physiologie der Pflanzen unter besonder Berücksichtigung der Forstgewächse. 308 s. J. Springer, Berlin.

——. 1894. Textbook of the diseases of trees. (Eng. trans. by SOMERVILLE and WARD.) 331 pp. Macmillan & Co., London.

HARTLEY, C. 1918. Stem lesions caused by excessive heat. *Jour. Agr. Research* **14**: 595–604.

——. 1921. Damping-off in forest nurseries. *U. S. Dept. Agr. Bul.* **934**. 99 pp.

——, T. C. MERRILL, and A. S. RHOADS. 1918. Seedling diseases of conifers. *Jour. Agr. Research* **15**: 521–558.

HATCH, A. B. 1936. The rôle of mycorrhizae in afforestation. *Jour. Forestry* **34**: 22–29.

——. 1937. The physical basis of mycotrophy in Pinus. *Black Rock Forest Bul.* **6**. 168 pp.

——, and K. D. Doak. 1933. Mycorrhizal and other features of the root systems of Pinus. *Jour. Arnold Arboretum* **14**:85–98.

Hatt, R. T. 1929. The red squirrel: Its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. *Roosevelt Wild Life Ann.* **2**(1): 11–146.

——. 1930. The biology of the voles of New York. *Roosevelt Wild Life Bul.* **5**(4): 513–623.

——. 1930. The relation of mammals to the Harvard Forest. *Roosevelt Wild Life Bul.* **5**(4): 625–671.

Haurwitz, B. 1941. Dynamic meteorology. 365 pp. McGraw-Hill Book Co., New York.

Hawley, R. C. 1922. A progress report of the results secured in treating white pine stands on experimental plots at Keene, New Hampshire. *Yale Univ. School Forestry Bul.* **7**. 32 pp.

——. 1937. Forest protection. 262 pp. John Wiley & Sons, New York.

——. 1946. The practice of silviculture. 5th Ed. 354 pp. John Wiley & Sons, New York.

Hayden, A. 1919. The ecologic subterranean anatomy of some plants of a prairie province in central Iowa. *Amer. Jour. Bot.* **6**:87–105.

Heimburger, C. C. 1934. Forest-type studies in the Adirondack region. *Cornell Univ. Agr. Expt. Sta. Mem.* **165**. 122 pp.

Heinicke, A. J. 1935. The apparent photosynthesis of an entire apple tree every day from pre-bloom to leaf fall, 1935. [Abs.] *Amer. Jour. Bot.* **22**: 903–904.

——, and M. B. Hoffman. 1933. The rate of photosynthesis of apple leaves under natural conditions. Pt. I. *Cornell Univ. Agr. Expt. Sta. Bul.* **577**. 32 pp.

Henry, A. 1919. Forests, woods, and trees in relation to hygiene. 314 pp. Constable & Co., London.

Henry, E. 1901. Sur le rôle de la forêt dans la circulation de l'eau a la surface des continents. *Rev. Eaux et Forêts* **40**:289–298, 321–333.

——. 1908. Les sols forestiers. 492 pp. Berger-Levrault & Cie, Paris.

Hesselman, H. 1917. Studier över saltpeterbildningen i naturliga jordmåner och dess betydelse i växtekologiskt avseende. (Studien über die nitratbildung in natürlichen Böden und ihre Bedeutung in pflanzenekologischer Hinsicht.) *Meddel. Statens Skogsförsöksanst.* **13–14**:297–527. (German summary pp. XXXIII–LVIII.)

——. 1926. Studier över barrskogens humustäcke, dess egenskaper och beroende av skogsvården. (Studien über die Humusdecke des Nadelwaldes, ihre Eigenschaften und deren Abhängigkeit vom Waldbau.) *Meddel. Statens Skogsförsöksanst.* **22**:169–507. (German summary pp. 508–552.)

Heyer, C., and R. Hess. 1906, 1909. Der Waldbau oder die Forstproduktenzucht. 2 Bd. 5 Aufl. 518 + 302 s. B. G. Teubner, Leipzig.

Heyer, G. 1852. Das Verhalten der Waldbäume gegen Licht und Schatten. 88 s. Erlangen.

Heyward, F., and R. M. Barnette. 1934. Effect of frequent fires on chemical composition of forest soils in the longleaf pine region. *Fla. Agr. Expt. Sta. Bul.* **265**. 39 pp.

——, and R. M. Barnette. 1936. Field characteristics and partial chemical analyses of the humus layer of longleaf pine forest soils. *Fla. Agr. Expt. Sta. Bul.* **302**. 27 pp.

——, and A. N. Tissot. 1936. Some changes in the soil fauna associated with forest fires in the longleaf pine region. *Ecology* **17**:659–666.

Hicock, H. W., M. F. Morgan, H. J. Lutz, H. Bull, and H. A. Lunt. 1931. The relation of forest composition and rate of growth to certain soil characters. *Conn. Agr. Expt. Sta. Bul.* **330**, pp. 675–750.

Hilgard, E. W. 1906. Soils: their formation, properties, composition, and relations to climate and plant growth in the humid and arid regions. 593 pp. The Macmillan Co., New York.

Hill, R. R. 1917. Effects of grazing upon western yellow pine reproduction in the national forests of Arizona and New Mexico. *U. S. Dept. Agr. Bul.* **580.** 27 pp.

Hirata, T. 1929. Contributions to the problem of the relation between the forest and water in Japan. 41 pp. Imp. Forestry Expt. Sta., Meguro, Tokyo, Japan.

Hoff, J. H. van't. 1887. Die Rolle des osmotischen Drückes in der Analogie zwischen Lösungen und Gasen. *Ztschr. Phys. Chem.* **1**:481–508.

Hofmann, J. V. 1917. Natural reproduction from seed stored in the forest floor. *Jour. Agr. Research* **11**:1–26.

——. 1921. Adaptation in Douglas fir. *Ecology* **2**:127–131.

——. 1924. The natural regeneration of Douglas fir in the Pacific Northwest. *U. S. Dept. Agr. Bul.* **1200.** 62 pp.

Höhnel, F. R. von. 1884. Ueber das Wasserbedürfniss der Wälder. *Centbl. Gesam. Forstw.* **10**:387–409.

Holch, A. E. 1931. Development of roots and shoots of certain deciduous tree seedlings in different forest sites. *Ecology* **12**:259–298.

Honcamp, F., et al. 1931. Handbuch der Pflanzenernährung und Düngerlehre. Bd. 1: Pflanzenernährung. 945 s. J. Springer, Berlin.

Honda, S. 1892. Eine Untersuchungsreihe über den Einfluss der Höhenlage der Gebirge auf die Veränderung des Zuwachses der Waldbäume. 27 s. J. D. Sauerländer's Verlag, Frankfurt am Main.

Hoover, W. H. 1937. The dependence of carbon dioxide assimilation in a higher plant on wave length of radiation. *Smithsn. Misc. Collect.* **95**(21): 1–13.

Hornaday, W. T. 1914. Wild life conservation in theory and practice. 240 pp. Yale Univ. Press, New Haven.

Hornibrook, E. M. 1939. A modified tree classification for use in growth studies and timber marking in Black Hills ponderosa pine. *Jour. Forestry* **37**:483–488.

Horton, R. E. 1919. Rainfall interception. *U. S. Mo. Weather Rev.* **47**:603–623.

Hosley, N. W. 1928. Red squirrel damage to coniferous plantations and its relation to changing food habits. *Ecology* **9**:43–48.

Howard, W. L. 1910. An experimental study of the rest period in plants: The winter rest. *Missouri Agr. Expt. Sta. Research Bul.* **1.** 105 pp.

Hubert, E. E. 1931. An outline of forest pathology. 543 pp. John Wiley & Sons, New York.

Huffaker, C. B. 1942. Vegetational correlations with vapor pressure deficit and relative humidity. *Amer. Midl. Nat.* **28**:486–500.

Huffel, G. 1904. Economie Forestière, Tome 1. 422 pp. Lucien Laveur, Paris.

——. 1912. Influence de la provenance des graines sur la qualité des plants de pin sylvestre. *Rev. Eaux et Forêts* **51**:673–682.

HUMBOLDT, A. VON. 1805. Essai sur la géographie des plantes. 155 pp. Levrault. Schoell et Cie., Paris.

HUMPHREYS, W. J. 1916. Wind velocity and elevation. *U. S. Mo. Weather Rev.* **44**: 14–17.

HUNTINGTON, E. 1914. The climatic factor as illustrated in arid America. *Carnegie Inst. Wash. Pub.* **192.** 341 pp.

——, and S. S. VISHER. 1922. Climatic changes: Their nature and causes. 329 pp. Yale Univ. Press, New Haven.

HURSH, C. R., and F. W. HAASIS. 1931. Effects of 1925 summer drought on southern Appalachian hardwoods. *Ecology* **12**: 380–386.

HUTCHINS, L. M. 1926. Studies on the oxygen-supplying power of the soil together with quantitative observations on the oxygen-supplying power requisite for seed germination. *Plant Physiol.* **1**: 95–150.

ILVESSALO, Y. 1926. Preparation of growth and yield tables. *Internatl. Inst. Agr. World Forestry Cong. Proc. Proof No.* **33.** 7 pp.

——. 1929. Notes on some forest (site) types in North America. *Acta Forest. Fennica* **34**(39): 1–111.

ISAAC, L. A. 1935. Life of Douglas fir seed in the forest floor. *Jour. Forestry* **33**: 61–66.

——. 1943. Reproductive habits of Douglas fir. 107 pp. Charles Lathrop Pack Forestry Found., Wash., D. C.

——, K. P. DAVIS, and R. H. WEIDMAN. 1941. Natural regeneration in the western white pine type. *U. S. Dept. Agr. Tech. Bul.* **767.** 99 pp.

JAENICKE, A. J., and M. J. FOERSTER. 1915. The influence of a western yellow pine forest on the accumulation and melting of snow. *U. S. Mo. Weather Rev.* **43**: 115–126.

JENNY, H. 1929. Climate and climatic soil types of Europe and United States. *Soil Research* **1**(3): 139–189.

——. 1930. The nitrogen content of the soil as related to the precipitation-evaporation ratio. *Soil Sci.* **29**: 193–206.

JOHANNSSON, N. 1926. Ökologische Studien über den Gasaustausch einiger Landpflanzen. *Svensk Bot. Tidskr.* **20**: 107–236.

JOHNSON, C. E. 1927. The beaver in the Adirondacks: Its economics and natural history. *Roosevelt Wild Life Bul.* **4**(4): 501–641.

JOHNSTON, E. S. 1932. The function of radiation in the physiology of plants. II. Some effects of near infra-red radiation on plants. *Smithsn. Misc. Collect.* **87**(14): 1–15.

——. 1934. Phototropic sensitivity in relation to wave length. *Smithsn. Misc. Collect.* **92**(11): 1–17.

——. 1936. Growth movements in relation to radiation. *In* Biological Effects of Radiation, pp. 1073–1091. Ed. by B. M. DUGGAR. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

JOFFE, J. S. 1936. Pedology. 575 pp. Rutgers Univ. Press, New Brunswick, N. J.

JOST, L. 1907. Lectures on plant physiology. (Eng. trans. by R. J. H. GIBSON.) 564 pp. Clarendon Press, Oxford.

JUDEICH, F., and M. NEUMEISTER. 1923. Die Forsteinrichtung. 8 Aufl. 607 s. P. Parey, Berlin.

KAMERLING, Z. 1914. Welche Pflanzen sollen wir Xerophyten nennen. *Flora* **106**: 433–454.

KEEN, B. A. 1928. The limited rôle of capillarity in supplying water to plant roots. *First Internatl. Cong. Soil Sci. (1927) Proc. and Papers* **1**: 504–511.

KEEN, F. P. 1936. Relative susceptibility of ponderosa pines to bark-beetle attack. *Jour. Forestry* **34**: 919–927.

——. 1943. Ponderosa pine tree classes redefined. *Jour. Forestry* **41**: 249–253.

——, and K. A. SALMAN. 1942. Progress in pine beetle control through tree selection. *Jour. Forestry* **40**: 854–858.

KELLEY, A. P. 1932. The literature of mycorrhizae. Manuscript, U. S. Dept. Agr. Library. 900 pp.

KELLOGG, F. B. 1915. Sand-dune reclamation on the coast of northern California and southern Oregon. *Soc. Amer. Foresters Proc.* **10**: 41–64.

KESSELL, S. L. 1927. The dependence of certain pine species on a biological soil factor. *Empire Forestry Jour.* **6**: 70–74.

KIENITZ, M. 1911. Formen und Abarten der gemeinen Kiefer (*Pinus sylvestris* L.) *Ztschr. Forst u. Jagdw.* **43**: 4–35.

KIMBALL, H. H. 1936. The intensity of solar radiation as received at the surface of the earth and its variations with latitude, altitude, the season of the year and the time of day. *In* Biological Effects of Radiation, pp. 211–226. Ed. by B. M. DUGGAR. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

KING, F. H. 1894. Destructive effects of winds on sandy soils and light sandy loams, with methods of protection. *Wis. Agr. Expt. Sta. Bul.* **42**. 29 pp.

KINZEL, W. 1915. Frost und Licht als beeinflussende Kräfte bei der Samenkeimung. *Naturw. Ztschr. Forstl. u. Landw.* **13**: 433–448.

KJELLMAN, F. R. 1885. VII. Aus dem Leben der Polarpflanzen. *In* "Studien und Forschungen veranlasst durch meine Reisen im hohen Norden," by N. A. E. NORDENSKIÖLD, pp. 443–521. F. A. Brockhaus, Leipzig.

KLEBS, G. 1914. Über das Treiben der einheimische Bäume, speziell der Buche. *Abh. d. Heidelberger Akad. d. Wiss., Math.-Naturw. Kl.* 3. Abh. Heidelberg. C. Winter.

KNUCHEL, H. 1914. Spektrophotometrische Untersuchungen im Walde. *Mitt. Schweiz. Centralanst. Forstl. Versuchsw.* **11**: 1–94.

KOPECKÝ, I. 1928. Investigations of the relations of water to soil. *First Internatl. Cong. Soil Sci. (1927) Proc. and Papers* **1**: 495–503.

KORSTIAN, C. F. 1917. The indicator significance of native vegetation in the determination of forest sites. *Plant World* **20**: 267–287.

——. 1919. Native vegetation as a criterion of site. *Plant World* **22**: 253–261.

——. 1921. Effect of a late spring frost upon forest vegetation in the Wasatch Mountains of Utah. *Ecology* **2**: 47–52.

——. 1921. Grazing practice on the national forests and its effect on natural conditions. *Sci. Mo.* **13**: 275–281.

——. 1921. Relation of precipitation to height growth of forest tree saplings. *Utah Acad. Sci. Trans.* **2**: 259–266.

——. 1923. Control of snow molding in coniferous nursery stock. *Jour. Agr. Research* **24**: 741–748.

——. 1924. Natural regeneration of southern white cedar. *Ecology* **5**: 188–191.

——. 1925. Density of cell sap in relation to environmental conditions in the Wasatch Mountains of Utah. *Jour. Agr. Research* **28**: 845–907.

——. 1925. Some ecological effects of shading coniferous nursery stock. *Ecology* **6**: 48–51.

——. 1927. Factors controlling germination and early survival in oaks. *Yale Univ. School Forestry Bul.* 19. 115 pp. New Haven.

——. 1933. Physico-chemical properties of leaves and leaf sap as indices of the water relations of forest trees. *Comptes rendus du Congres de Nancy, 1932 de l'Union internationale des Instituts de Recherches forestieres,* pp. 312–325.

——. 1934. Plant competition under forest canopies. [Abs.] *Bul. Ecological Soc. Amer.* 15:39.

——. 1937. Perpetuation of spruce on cut-over and burned lands in the higher Southern Appalachian Mountains. *Ecological Monog.* 7:125–167.

——, and F. S. Baker. 1922. Is Douglas fir replacing western yellow pine in central Idaho? *Jour. Forestry* 22:755–764.

——, and F. S. Baker. 1925. Forest planting in the Intermountain region. *U. S. Dept. Agr. Bul.* 1264. 57 pp.

——, and W. D. Brush. 1931. Southern white cedar. *U. S. Dept. Agr. Bul.* 251. 76 pp.

——, and T. S. Coile. 1938. Plant competition in forest stands. *Duke Univ. School Forestry Bul.* 3. 125 pp.

——, and N. J. Fetherolf. 1921. Control of stem girdle of spruce transplants caused by excessive heat. *Phytopathology* 11:485–490.

——, C. Hartley, L. F. Watts, and G. G. Hahn. 1921. A chlorosis of conifers corrected by spraying with ferrous sulphate. *Jour. Agr. Research* 21:153–171.

——, and W. Maughan. 1935. The Duke Forest: A demonstration and research laboratory. *Duke Univ. Forestry Bul.* 1. 74 pp.

——, and P. W. Stickel. 1927. The natural replacement of blight-killed chestnut in the hardwood forests of the Northeast. *Jour. Agr. Research* 34:631–648.

——, and P. W. Stickel. 1927. The natural replacement of blight-killed chestnut. *U. S. Dept. Agr. Misc. Circ.* 100. 15 pp.

Kostychev, S. 1931. Kostychev's chemical plant physiology. 497 pp. (Eng. trans. by C. J. Lyon.) P. Blakiston's Son & Co., Philadelphia.

Kramer, P. J. 1934. Effects of soil temperature on the absorption of water by plants. *Science N. S.* 79:371–372.

——. 1934. Methods of breaking dormancy in certain forest trees. *Jour. Forestry* 32:734–741.

——. 1936. Effect of variation in length of day on growth and dormancy of trees. *Plant Physiol.* 11:127–137.

——. 1944. Soil moisture in relation to plant growth. *Bot. Rev.* 10:525–559.

——. 1945. Absorption of water by plants. *Bot. Rev.* 11:310–355.

——, and J. P. Decker. 1944. Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. *Plant Physiol.* 19:350–358.

Kunkel, L. O. 1912. A study of the problem of water absorption. *Rpt. Missouri Bot. Gard.* 23:26–40.

Kurz, H., and D. Demaree. 1934. Cypress buttresses and knees in relation to water and air. *Ecology* 15:36–41.

Lang, R. 1932. Der Humus als Ganzes. *Forstw. Centbl.* 54:389–405.

——. 1932. Entwicklungsrichtung des Humus. *Forstw. Wochenschr. Silva* 20:185–190, 193–195.

Lebedeff, A. F. 1928. The movement of ground and soil waters. *First Internatl. Cong. Soil Sci. (1927) Proc. and Papers* 1:459–494.

LEOPOLD, A. 1924. Grass, brush, timber, and fire in southern Arizona. *Jour. Forestry* 22(6): 1–10. (Misnumbered pages in Oct. number.)

——. 1930. Environmental controls for game through modified silviculture. *Jour. Forestry* **28**: 321–326.

——. 1931. Report on a game survey of the north central states. 299 pp. Sporting Arms and Ammunition Manufacturers' Institute, Madison.

——. 1933. Game management. 481 pp. Charles Scribner's Sons, New York.

LI, T. T. 1926. Soil temperature as influenced by forest cover. *Yale Univ. School Forestry Bul.* **18.** 92 pp.

——. 1928. The effect of intense sunlight on tree seedlings. *Lignan Sci. Jour.* **6**: 315–321.

LIEBIG, J. VON. 1855. Die Grundsätze der Agricultur-chemie, mit Rücksicht auf die in England angestellten Untersuchungen. 152 s. F. Vieveg und Sohn, Braunschweig.

LINFORD, L. B. 1926. The relation of light to soil moisture phenomena. *Soil Sci.* **22**: 233–251.

LINSBAUER, L. 1901. Untersuchungen über die Durchleuchtung von Laubblattern. *Bot. Centbl., Beihefte* **10**: 53–89.

LIPPINCOTT, J. B. 1899. Water supply of San Bernadino Valley. *U. S. Geol. Survey, 19th Ann. Rpt., Part IV.*, pp. 540–632.

LIPPMAA, T. 1929. Pflanzenökologische Untersuchungen aus Norwegisch- und Finnisch-Lappland unter besonderer Berücksichtigung der Lichtfrage. *Acta Inst. Hort. Bot. Univ. Tartuensis (Dorpatensis)* **2.** Fasc. 1–2. 1–146. [19] pp.

LIVINGSTON, B. E. 1905. The relation of soils to natural vegetation in Roscommon and Crawford Counties, Michigan. *Bot. Gaz.* **39**: 22–41.

——. 1913. The resistance offered by leaves to transpirational water loss. *Plant World* **16**: 1–35.

——, and R. KOKETSU. 1920. The water-supplying power of the soil as related to the wilting of plants. *Soil Sci.* **9**: 469–485.

——, and F. SHREVE. 1921. The distribution of vegetation in the United States as related to climatic conditions. *Carnegie Inst. Wash. Pub.* **284.** 590 pp.

LODJKIN, M. 1931. Some effects of ultraviolet rays on the vitamin D content of plants as compared with the direct irradiation of the animal. *Boyce Thompson Inst. Contrib.* **3**: 245–265.

LOWDERMILK, W. C. 1930. Further studies of factors affecting surficial run-off and erosion. *Verhandl. Internatl. Kong. Forstl. Versuchsanst. Stockholm 1929*, pp. 606–628.

——. 1930. Influence of forest litter on run-off, percolation, and erosion. *Jour. Forestry* **28**: 474–491.

——. 1933. Studies in the rôle of forest vegetation in erosion control and water conservation. *Fifth Pac. Sci. Cong., Canada, Proc.* **5**: 3963–3990.

——. 1934. The rôle of vegetation in erosion control and water conservation. *Jour. Forestry* **32**: 529–536.

LUBIMENKO, W. 1908. La concentration du pigment vert et l'assimilation chlorophyllienne. *Rev. Gen. Bot.* **20**: 162–177.

LUNDBLAD, K. 1934. Studies on podsols and brown forest soils: I. *Soil Sci.* **37**: 137–155.

LUNDEGÅRDH, H. 1922. Zur Physiologie und Ökologie der Kohlensäureassimilation. *Biol. Zentbl.* **42**: 337–358.

——. 1930. Klima und Boden in ihrer Wirkung auf das Pflanzenleben. 2 Aufl. 480 s. G. Fischer, Jena.

——. 1931. Environment and plant development. ("Klima und Boden in ihrer Wirkung auf das Pflanzenleben." Trans. from 2nd German Ed. by E. ASHBY.) 330 pp. Edward Arnold & Co., London.

LUNT, H. A. 1932. Profile characteristics of New England forest soils. *Conn. Agr. Expt. Sta. Bul.* **342,** pp. 741–836.

——. 1933. Effect of weathering upon composition of hardwood leaves. *Jour. Forestry* **31**: 943–945.

——. 1934. Distribution of soil moisture under isolated forest trees. *Jour. Agr. Research* **49**: 695–703.

LUTZ, H. J. 1934. Ecological relations in the pitch pine plains of southern New Jersey. *Yale Univ. School Forestry Bul.* **38.** 80 pp.

——. 1945. Vegetation on a trenched plot twenty-one years after establishment. *Ecology* **26**: 200–202.

LUTZ, J. F. 1934. The physico-chemical properties of soils affecting soil erosion. *Mo. Agr. Expt. Sta. Research Bul.* **212.** 45 pp.

MCATEE, W. L. 1925. Notes on drift, vegetable balls, and aquatic insects as a food product of inland waters. *Ecology* **6**: 288–302.

——. 1926. The relation of birds to woodlots in New York State. *Roosevelt Wild Life Bul.* **4**(1): 7–152.

MACDOUGAL, D. T. 1921. The reactions of plants to new habitats. *Ecology* **2**: 1–20.

——. 1936. Studies in tree-growth by the dendrographic method. *Carnegie Inst. Wash. Pub.* **462.** 256 pp.

——, and F. SHREVE. 1924. Growth in trees and massive organs of plants. *Carnegie Inst. Wash. Pub.* **350.** 116 pp.

MCDOUGALL, W. B. 1914. On the mycorrhizas of forest trees. *Amer. Jour. Bot.* **1**: 51–74.

——. 1922. Mycorrhizas of coniferous trees. *Jour. Forestry* **20**: 255–260.

——. 1922. Symbiosis in a deciduous forest. *Bot. Gaz.* **73**: 200–212.

——. 1927. Mycorrhizas from North Carolina and Eastern Tennessee. *Amer. Jour. Bot.* **15**: 141–148.

MCGEE, W. J. 1911. Principles of water power development. *Science N. S.* **34**: 813–825.

MACKINNEY, A. L. 1929. Effects of forest litter on soil temperature and soil freezing in autumn and winter. *Ecology* **10**: 312–321.

MCQUILKIN, W. E. 1935. Root development of pitch pine, with some comparative observations on shortleaf pine. *Jour. Agr. Research* **51**: 983–1016.

MAGISTAD, O. C., and J. F. BREAZEALE. 1929. Plant and soil relations at and below the wilting percentage. *Ariz. Agr. Expt. Sta. Tech. Bul.* **25.** 36 pp.

MARBUT, C. F. 1921. The contribution of soil surveys to soil science. *Soc. Prom. Agr. Sci. Proc.* **41**: 116–142.

——. 1922. Soil classification report. *Amer. Assoc. Soil Survey Workers Ann. Rpt.* **2**: 24–33.

——. 1928. A scheme for soil classification. *First Internatl. Cong. Soil Sci. (1927) Proc. and Papers* **4**: 1–31.

——. 1935. Soils of the United States. *In* Atlas of American Agriculture, Pt. III. 98 pp. U. S. Dept. Agr., Bur. Chem. and Soils. Wash., D. C.

MARSH, G. P. 1882. The earth as modified by human action. 674 pp. Charles Scribner's Sons, New York.

MARTIN, E. V., and F. E. CLEMENTS. 1935. Studies of the effect of artificial wind on growth and transpiration in *Helianthus annuus*. *Plant Physiol.* **10**: 613–636.

MASON, D. T. 1915. The life history of lodgepole pine in the Rocky Mountains. *U. S. Dept. Agr. Bul.* **154.** 35 pp.

——. 1915. Utilization and management of lodgepole pine in the Rocky Mountains. *U. S. Dept. Agr. Bul.* **234.** 54 pp.

MASTERS, M. T. 1891. Review of some points in the comparative morphology, anatomy, and life-history of the *Coniferae*. *Jour. Linn. Soc.* [*London*], *Bot.* **27**: 226–332.

MATTOON, W. R. 1936. Forest trees and forest regions of the United States. *U. S. Dept. Agr. Misc. Circ.* **217.** 54 pp.

MATTSON, S. 1932. The laws of soil colloidal behavior. VIII. Forms and functions of water. *Soil Sci.* **33**: 301–323.

MAXIMOV, N. A. 1929. The plant in relation to water: a study of the physiological basis of drought resistance. (Eng. trans. by R. H. YAPP.) 451 pp. George Allen & Unwin, London.

——. 1931. The physiological significance of the xeromorphic structure of plants. *Jour. Ecology* **19**: 273–283.

——, and T. A. KRASNOSELSKY-MAXIMOV. 1924. Wilting and drought resistance. *Jour. Ecology* **12**: 95–110.

——, and E. LEBENDINTSEV. 1923. Über den Einfluss von Beleuchtungsverhältnissen auf die Entwicklung des Wurzelsystems. *Ber. Deut. Bot. Gesell.* **41**: 292–297.

MAYR, H. 1925. Waldbau auf naturgesetzlicher Grundlage. 2 Aufl. 568 s. P. Parey, Berlin.

MEAD, D. W. 1911. The flow of streams and the factors which modify it, with special reference to Wisconsin conditions. *Univ. Wis. Bul.* **425.** 192 pp.

MEGINNIS, H. G. 1935. Effect of cover on surface run-off and erosion in the loessial uplands of Mississippi. *U. S. Dept. Agr. Circ.* **347.** 16 pp.

MEINECKE, E. P. 1916. Forest pathology in forest regulation. *U. S. Dept. Agr. Bul.* **275.** 62 pp.

MEINECKE, TH., D. J. 1927. Die Kohlenstoffernährung des Waldes. 176 s. J. Springer, Berlin.

MELIN, E. 1925. Untersuchungen über die Bedeutung der Baummykorrhiza. 152 s. Gustav Fisher, Jena.

——. 1927. Studier över barrträdsplantans utveckling i råhumus. II. Mykorrhizans utbildning hos tallplantan i olika råhumusformer. (Studien über die Entwicklung der Nadelbaumpflanze in Rohhumus. II. Die Ausbildung der Mykorrhiza bei der Kiefernpflanze in verschiedenen Rohhumusformen.) *Meddel. Statens Skogsförsöksanst.* **23**: 433–486. (German summary, pp. 487–494.)

——. 1930. Biological decomposition of some types of litter from North American forests. *Ecology* **11**: 72–101.

MERRIAM, C. H. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Nat. Geogr. Mag.* **6**: 229–238.

——. 1898. Life zones and crop zones of the United States. *U. S. Dept. Agr., Div. Biol. Survey Bul.* **10.** 79 pp. Wash., D. C.

MEYER, A. 1926. Über einige Zusammenhänge zwischen Klima und Boden in Europa. *Chemie der Erde* **2**: 209–347.

MEYER, B. S. 1928. Seasonal variations in the physical and chemical properties of the leaves of the pitch pine, with especial reference to cold resistance. *Amer. Jour. Bot.* **15**: 449–472.

MIDDENDORFF, A. T. VON. 1853. Reise in den äussersten norden und osten Siberiens während der Jahre 1843 und 1844. 516 pp. Buchdr. der K. Akademie der Wissenschaften, St. Petersburg.

MILLER, E. C. 1938. Plant physiology; with reference to the green plant. 2nd Ed. 1201 pp. McGraw-Hill Book Co., New York.

MILLER, J. P. 1935. The correlation of game and forest management in New England. *Trans. 21st Amer. Game Conf., New York*, pp. 309–312.

MITCHELL, H. L., R. F. FINN, and R. O. ROSENDAHL. 1937. The relation between mycorrhizae and the growth and nutrient absorption of coniferous seedlings in nursery beds. *Black Rock Forest Papers* **1**(10), pp. 57–73.

MITSCHERLICH, E. A. 1909. Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenertrages. *Landw. Jahrb.* **38**: 537–552.

——. 1921. Das Wirkungsgesetz der Wachstumfaktoren. *Landw. Jahrb.* **56**: 71–92.

MÖLLER, A. 1906. Mykorhizen und Stickstoffernährung. *Ber. Deut. Bot. Gesell.* **24**: 230–233.

——. 1912. Demonstration und Vortrag im Versuchsgarten der mykologischen Abteilung (Jagen 106, Oberförsterei Eberswalde.) *Ztschr. Forst u. Jagdw.* **44**: 330–332.

——. 1929. Der Waldbau: Vorlesungen für Hochschul-Studenten. 1 Bd. (Nach dem Tode Alfred Möllers bearbeitet und herausgegeben von Helen Möller und Erhard Hausendorff.) 560 s. J. Springer, Berlin.

MOORE, B. 1922. Humus and root systems in certain northeastern forests in relation to reproduction and competition. *Jour. Forestry* **20**: 233–254.

——. 1926. Influence of certain soil and light conditions on the establishment of reproduction in northeastern conifers. *Ecology* **7**: 191–220.

——. 1928. Measurement of the water-supplying power of the soil. *Ecology* **9**: 530–532.

MOORE, W. L. 1911. Descriptive meteorology. 344 pp. D. Appleton & Co., New York.

MOSS, C. E. 1907. Succession of plant formations in Britain. *Brit. Assoc. Adv. Sci. Rpt. York, 1906.* pp. 742–743.

——. 1910. The fundamental units of vegetation: Historical development of the concepts of the plant association and the plant formation. *New Phytol.* **9**: 18–53.

MÜLLER, P. E. 1887. Studien über die naturlichen Humusformen und deren Einwirkung auf Vegetation und Boden. 324 pp. J. Springer, Berlin.

MUNDT, H. 1934. Aims and means in the forest: good forests and thinnings. *Scot. Forestry Jour.* **48**: 121–141.

MUNGER, T. T. 1911. Avalanches and forest cover in the northern Cascades. *U. S. Dept. Agr., Forest Serv. Circ.* **173.** 12 pp.

——. 1913. Shall the physical conditions or the dendrological mixture be the basis for forest typing? *Soc. Amer. Foresters Proc.* **8**: 62–68.

MUNNS, E. N., and I. H. SIMS. 1936. Forests in flood control. 70 pp. *Sup. Rpt. to Com. on Flood Control, House Represent., 74th Cong., 2nd Sess., on H. R. 12517.* Wash., D. C.

NANSEN, F. 1914. Through Siberia, the land of the future. (Eng. trans. by A. G. CHATER.) 478 pp. W. Heineman Ballantyne Press, London.

National Conservation Congress. 1913. The relation of forests and water. *Rpt. Forestry Com., Fifth Natl. Conservation Cong.* pp. 184–204. Wash., D. C.

NEY, C. E. 1894. Der Wald und die Quellen. 101 pp. Sonderabdruck aus "Aus dem Walde." Tübingen.

——. 1901. Der Wald und die Quellenbildung. *Forstwiss. Centbl.* **23**: 440–463.

NICHOLS, G. E. 1917. The interpretation and application of certain terms and concepts in the ecological classification of plant communities. *Plant World* **20**: 305–319, 341–353.

——. 1923. A working basis for the ecological classification of plant communities. *Ecology* **4**: 11–23, 154–179.

NISBET, J. 1893. On mixed forests and their advantages over pure forests. 30 pp. Eyre and Spottiswoode, London.

——. 1893. Soil and situation in relation to forest growth. 31 pp. Eyre and Spottiswoode, London.

——. 1894. Studies in forestry. 335 pp. Clarendon Press, Oxford.

OLMSTEAD, L. B., L. T. ALEXANDER, and H. E. MIDDLETON. 1930. A pipette method of mechanical analysis of soils based on improved dispersion procedure. *U. S. Dept. Agr. Tech. Bul.* **170.** 22 pp.

OOSTING, H. J., and P. J. KRAMER. 1946. Water and light in relation to pine reproduction. *Ecology* **27**: 47–53.

PALLADIN, V. I. 1926. Palladin's plant physiology. 3rd Ed. Edited by B. E. LIVINGSTON. 360 pp. P. Blakiston's Son & Co., Philadelphia.

PARK, O. 1931. The measurement of daylight in the Chicago area and its ecological significance. *Ecological Monog.* **1**: 189–230.

PARKER, R. W. 1922. The classification of soil moisture. *Soil Sci.* **13**: 43–54.

PAVILLARD, J. 1935. The present status of the plant association. *Bot. Rev.* **1**: 210–232.

PEARSE, A. S. 1939. Animal ecology. 2nd Ed. 642 pp. McGraw-Hill Book Co., New York.

PEARSE, G. W., and L. R. STREETER. 1931. A report on the effect of light on pigment formation in apples. *Jour. Biol. Chem.* **92**: 743–749.

PEARSON, G. A. 1914. A meteorological study of parks and timbered areas in the western yellow pine forests of Arizona and New Mexico. *U. S. Mo. Weather Rev.* **41**: 1615–1629.

——. 1918. The relation between spring precipitation and height growth of western yellow pine saplings in Arizona. *Jour. Forestry* **16**: 677–689.

——. 1920. Factors controlling the distribution of forest types. *Ecology* **1**: 139–159, 289–308.

——. 1923. Natural reproduction of western yellow pine in the southwest. *U. S. Dept. Agr. Bul.* **1105.** 143 pp.

——. 1929. The other side of the light question. *Jour. Forestry* **27**: 807–812.

——. 1930. Light and moisture in forestry. *Ecology* **11**: 145–160.

——. 1931. Forest types in the southwest as determined by climate and soil. *U. S. Dept. Agr. Tech. Bul.* **247.** 144 pp.

——. 1936. Some observations on the reaction of pine seedlings to shade. *Ecology* **17**: 270–276.

PETTERSSEN, S. 1940. Weather analysis and forecasting. 505 pp. McGraw-Hill Book Co., Inc., New York.

PFEFFER, W. F. P. 1877. Osmotische Untersuchungen. 236 pp. W. Engelmann, Leipzig.

PHILLIPS, J. F. V. 1926. Rainfall interception by plants. *Nature* **118**: 837–838.

PHILLIPS, J. 1934, 1935. Succession, development, the climax, and the complex organism: an analysis of concepts. *Jour. Ecology* **22**: 554–571; **23**: 210–246, 488–508.

PIKE, G. W. 1934. Girdling of ponderosa pine by squirrels. *Jour. Forestry* **32**: 98–99.

PISTON, D. S. 1931. Meteorology. 187 pp. P. Blakiston's Son & Co., Philadelphia.

PLICE, M. J. 1934. Acidity, antacid buffering, and nutrient content of forest litter in relation to humus and soil. *Cornell Univ. Agr. Expt. Sta. Mem.* **166.** 32 pp.

PLUMMER, F. G. 1912. Lightning in relation to forest fires. *U. S. Dept. Agr., Forest Serv. Bul.* **111.** 39 pp.

POPP, H. W. 1926. A physiological study of the effect of light of various ranges of wave length on the growth of plants. *Amer. Jour. Bot.* **13**: 706–736.

——, and F. BROWN. 1936. Effects of different regions of the visible spectrum upon seed plants. *In* Biological Effects of Radiation, pp. 763–790. Ed. by B. M. DUGGAR. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

POUND, R., and F. E. CLEMENTS. 1900. The phytogeography of Nebraska. 2nd Ed. 442 pp. Nebr. Univ., Bot. Seminar, Bot. Surv. Nebr., Lincoln.

POWERS, W. L. 1932. Characteristics of forest soils of the northwestern United States. *Soil Sci.* **34**: 1–10.

PRESTON, C. E. 1901. Structural studies on southwestern *Cactaceae*. *Bot. Gaz.* **32**: 35–55.

PULLING, H. E. 1919. Sunlight and its measurement. *Plant World* **22**: 151–171, 187–209.

RAMALEY, F. 1933. A working bibliography of day-length and artificial illumination as affecting growth of seed plants. *Univ. Colo. Studies* **20**: 257–263.

RAMANN, E. 1905. Bodenkunde, 2 Aufl., 431 s. J. Springer, Berlin.

——. 1928. The evolution and classification of soils. (Trans. by C. L. WHITTES.) 128 pp. W. Heffer & Sons, Cambridge (Eng.).

RANKIN, W. H. 1918. Manual of tree diseases. 398 pp. The Macmillan Co., New York.

RAUNKIÄER, C. 1905. Types biologiques pour la geographie botanique. *Overs. K. Danske Vidensk. Selsk. Forh.* S. 347–437.

——. 1934. The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer. 632 pp. Clarendon Press, Oxford.

RAYNER, M. C. 1934. Mycorrhiza in relation to forestry. I. Researches on the genus *Pinus* with an account of experimental work on a selected area. *Forestry* **8**: 96–125.

——. 1936. The mycorrhizal habit in relation to forestry. II. Organic composts and the growth of young trees. *Forestry* **10**: 1–22.

——, and W. Neilson-Jones. 1944. Problems in tree nutrition. 184 pp. Faber and Faber, Ltd., London.

Reed, J. F. 1939. Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. *Duke Univ. School Forestry Bul.* **4.** 52 pp.

Renner, F. G. 1936. Conditions influencing erosion on the Boise River watershed. *U. S. Dept. Agr. Tech. Bul.* **528.** 32 pp.

Rhoades, V., and W. W. Ashe. 1918. Ice storms in the Southern Appalachians. *U. S. Mo. Weather Rev.* **46**: 373–374.

Rigg, G. B., and E. S. Harrar. 1931. The root systems of trees growing in sphagnum. *Amer. Jour. Bot.* **18**: 391–397.

——, and T. G. Thompson. 1919. Colloidal properties of bog water. *Bot. Gaz.* **68**: 367–379.

Robinson, G. W. 1932. Soils: Their origin, constitution and classification: an introduction to pedology. 390 pp. Thomas Murby & Co., London.

Robinson, W. O. 1922. The absorption of water by soil colloids. *Jour. Phys. Chem.* **26**: 647–653.

Romell, L. G. 1926. Über das Zusammenwirken der Productionsfaktoren. *Jahrb. Wiss. Bot.* **65**: 739–777.

——. 1935. An example of myriapods as mull formers. *Ecology* **16**: 67–71.

——. 1935. Ecological problems of the humus layer in the forest. *Cornell Univ. Agr. Expt. Sta. Mem.* **170.** 28 pp.

——, and S. O. Heiberg. 1931. Types of humus layer in the forests of northeastern United States. *Ecology* **12**: 567–608.

Rosé, E. 1913. Énergie assimilatrice chez les plantes cultivées sous différents éclairements. *Ann. Sci. Nat. Bot. IX*, **17**: 1–110.

Roth, F. 1916. Concerning site. *Forestry Quart.* **14**: 3–13.

Rubner, K. 1934. Die pflanzengeographische-ökologischen Grundlagen des Waldbaus. 3 Aufl. 597 s. J. Neumann, Neudamm.

Russell, E. J. 1926. Plant nutrition and crop production. 115 pp. Univ. Calif. Press, Berkeley.

——. 1932. Soil conditions and plant growth. 6th Ed. 636 pp. Longmans, Green & Co., London.

Sachs, J. 1865. Handbuch der Experimental-Physiologie der Pflanzen. 514 s. Wilhelm Engelmann, Berlin.

Salisch, H. von. 1911. Forstästhetik. 3 Aufl. 434 s. J. Springer, Berlin.

Sampson, A. W. 1919. Effect of grazing upon aspen reproduction. *U. S. Dept. Agr. Bul.* **741.** 29 pp.

Sarauw, G. F. L. 1893. Rodsymbiose og Mykorrhizer særlig hos Skovtræerne. *Bot. Tidsskr.* **18**: 127–259.

Sargent, C. S. 1884. Report on the forests of North America (exclusive of Mexico). 612 pp. U. S. Dept. Int., Census Off., Washington.

Sayre, J. D. 1928. The development of chlorophyll in seedlings in different ranges of wave lengths of light. *Plant Physiol.* **3**: 71–77.

Schantz, F. 1918. Einfluss des Lichts auf die Gestaltung der Vegetation. *Ber. Deut. Bot. Gesell.* **36**: 619–626.

——. 1919. Wirkung des Lichtes verschiedener Wellenlänge auf die Pflanzen. *Ber. Deut. Bot. Gesell.* **37**: 430–442.

Scharfetter, R. 1922. Klimarhythmik, Vegetationrhythmik, und Formationsrhythmik. *Österr. Bot. Ztschr.* **71**: 153–171.

——. 1928. Die kartographische Darstellung der Pflanzengesellschaften. *Handb. Biol. Arbeitsmeth. Abderhalden XI.* **5**: 77–164.

SCHIMPER, A. F. W. 1903. Plant geography upon a physiological basis. 839 pp. (Eng. trans. by W. R. FISHER.) (Rev. and ed. by P. GROOM and I. B. BALFOUR.) Clarendon Press, Oxford.

SCHLICH, W. 1895, 1896, 1897, 1910, 1911. A manual of forestry: Vol 1. Introduction to forestry. 2nd. Ed. 294 pp. 1896. Vol. 2. Silviculture. 4th Ed. 424 pp. 1910. Vol. 3. Forest Management. 4th Ed. 403 pp. 1911. Vol. 4. Forest Protection. By W. R. FISHER. 593 pp. 1895. Vol. 5. Forest Utilization. By W. R. FISHER. 779 pp. 1896. Bradbury, Agnew & Co., London.

SCHMIDT, J. 1905. Bidrag til Kundskab om Skuddene hos den gamle Verdens Mangrovetrâeer. *Bot. Tidsskr.* **26**: 1–113.

SCHMIDT, W. 1930. Unsere Kenntnis vom Forstsaatgut. 256 pp. Verlag "Der Deutsche Forstwirt," Berlin.

SCHOLZ, H. F. 1931. Physical properties of the cove soils on the Black Rock Forest. *Black Rock Forest Bul.* **2**. 59 pp.

SCHRENCK, H. VON, and P. SPAULDING. 1909. Diseases of deciduous forest trees. *U. S. Dept. Agr., Bur. Plant Indus. Bul.* **149**. 85 pp.

SCHUBERT, J. O. 1900. Der jährliche Gang der Luft- und Boden-temperatur im Freien und in Waldungen und der Wärmeaustausch im Erdboden. 53(1) pp. J. Springer, Berlin.

SCHÜTZE, W. 1871. Beziehungen zwischen chemischer Zusammensetzung und Ertragsfähigkeit des Waldbodens. *Ztschr. Forst u. Jagdw.* **3**: 367–390.

SETCHELL, W. A. 1925. Temperature and anthesis. *Amer. Jour. Bot.* **12**: 178–188.

SEYBOLD, A. 1932–1934. Über die optischen Eigenschaften der Laubblätter. *Planta Arch. Wiss. Bot.* I, **16**:195–226, 1932; II, **18**:479–508, 1933; III, **20**: 577–601, 1933; IV, **21**: 251–265, 1934.

SHANTZ, H. L. 1911. Natural vegetation as an indicator of the capabilities of land for crop production. *U. S. Dept. Agr., Bur. Plant Ind. Bul.* **201**. 100 pp.

——. 1913. The effects of artificial shading on plant growth in Louisiana. *U. S. Dept. Agr., Bur. Plant Indus. Bul.* **279**. 31 pp.

——. 1927. Drought resistance and soil moisture. *Ecology* **8**: 145–157.

——, and R. ZON. 1924. The physical basis of agriculture: Natural vegetation. *In* Atlas of American agriculture, Pt. I, Sect. E. 29 p. U. S. Dept. Agr., Bur. Agr. Economics, Wash., D. C.

SHAW, C. F., and A. SMITH. 1927. Maximum height of capillary rise starting with soil at capillary saturation. *Hilgardia* **2**: 399–409.

SHEAR, G. M., and W. D. STEWART. 1934. Moisture and pH studies of the soil under forest trees. *Ecology* **15**: 145–153.

SHEFF, E. E. 1913. Evaporation and the stratification of vegetation. *Plant World* **16**: 154–160.

SHELFORD, V. E. 1929. Laboratory and field ecology: the responses of animals as indicators of correct working methods. 608 pp. Williams & Wilkins Co., Baltimore.

SHEPARD, W. 1928. Forest and floods. *U. S. Dept. Agr. Circ.* **19**. 24 pp.

SHERMAN, E. A., et al. 1929. Relation of forestry to the control of floods in the Mississippi Valley. 740 pp. *House Doc. 573, 70th Cong., 2nd Sess., Wash., D. C.*

SHIRLEY, H. L. 1929. The influence of light intensity and light quality upon the growth of plants. *Amer. Jour. Bot.* **16**:354–390.

——. 1929. Light requirements and silvicultural practice. *Jour. Forestry* **27**: 535–538.

——. 1930. A thermoelectric radiometer for ecological use on land and in water. *Ecology* **11**:61–71.

——. 1931. The influence of light and temperature upon the utilization by young seedlings of organic reserves in the seed. *Amer. Jour. Bot.* **18**:717–727.

——. 1931. Light sources and light measurements. *Plant Physiol.* **6**:447–466.

——. 1932. Light and moisture as factors in forest succession. [Abs.] *Bul. Ecological Soc. Amer.* 13(4): Abs. 31 [p. 12].

——. 1932. Light intensity in relation to plant growth in a virgin Norway pine forest. *Jour. Agr. Research* **44**:227–244.

——. 1934. Observations on drought injury in Minnesota. *Ecology* **15**:42–48.

——. 1935. Light as an ecological factor and its measurement. *Bot. Rev.* **1**: 355–381.

——. 1936. The effects of light intensity upon seed plants. *In* Biological Effects of Radiation, pp. 727–762. Ed. by B. M. DUGGAR. 2 vols. 1343 pp. McGraw-Hill Book Co., New York.

——. 1936. Lethal high temperatures for conifers, and the cooling effect of transpiration. *Jour. Agr. Research* **53**:239–258.

——. 1936. The utilization of solar radiation by forests. *Bul. Amer. Met. Soc.* **17**:64–67.

——. 1943. Is tolerance the capacity to endure shade? *Jour. Forestry* **41**: 339–345.

——. 1945. Reproduction of upland conifers in the Lake States as affected by root competition and light. *Amer. Midl. Nat.* **33**:537–612.

SHIVE, J. W., and B. E. LIVINGSTON. 1914. The relation of atmospheric evaporating power to soil moisture content at permanent wilting in plants. *Plant World* **17**:81–121.

SHOW, S. B., and E. I. KOTOK. 1923. The occurrence of lightning storms in relation to forest fires in California. *U. S. Mo. Weather Rev.* **51**:175–182.

——, and E. I. KOTOK. 1924. The rôle of fire in the California pine forests. *U. S. Dept. Agr. Bul.* **1294**. 80 pp.

SHREVE, F. 1911. Establishment behavior of the palo verde. *Plant World* **14**: 289–296.

——. 1912. Cold-air drainage. *Plant World* **15**:110–115.

——. 1914. The rôle of winter temperatures in determining the distribution of plants. *Amer. Jour. Bot.* **1**:194–202.

——. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. *Carnegie Inst. Wash. Pub.* **217**. 112 pp.

——. 1917. A map of the vegetation of the United States. *Geogr. Rev.* **3**: 119–125.

——. 1924. Soil temperature as influenced by altitude and slope exposure. *Ecology* **5**:128–136.

SHULL, C. A. 1919. Correlation of windflow and temperature with evaporation. *Plant World* **22**:210–215.

——. 1928. Reflection of light from the surfaces of leaves. *Science N. S.* **67**: 107–108.

——. 1929. A spectroscopic study of reflection of light from leaf surfaces. *Bot. Gaz.* **87**: 583–607.

Sibirtsev, N. M. 1900. Pochvovedenie [Pedology]. St. Petersburg.

Siggins, H. W. 1933. Distribution and rate of fall of conifer seeds. *Jour. Agr. Research* **47**: 119–128.

Silcox, F. A., et al. 1935. Possibilities of shelterbelt planting in the plains region. 201 pp. U. S. Dept. Agr., Forest Service, Wash., D. C.

Silloway, P. M. 1923. Relation of summer birds to the western Adirondack forest. *Roosevelt Wild Life Bul.* 1(4): 397–486.

Simpson, W. 1927. The seasonal variation of soil moisture in the forest and in the open. Yale Univ. Ph. D. thesis (unpublished).

Sisam, J. W. B. 1938. Site as a factor in silviculture: Its determination with special reference to the use of plant indicators. Canada Dept. Mines and Resources; Lands, Parks and Forests Branch, *Silvicultural Research Note* **54**. 88 pp. (Processed), Ottawa.

Skeen, J. R. 1925. A critical pH for the formation of hardpan in acid clay soils. *Soil Sci.* **20**: 307–311.

Skene, M. 1924. The biology of flowering plants. 523 pp. The Macmillan Co., New York.

Slater, C. S., and H. G. Byers. 1931. A laboratory study of the field percolation rates of soils. *U. S. Dept. Agr. Tech. Bul.* **232**. 23 pp.

Society of American Foresters. 1923. Classification of forest sites. (Com. Rpt.) *Jour. Forestry* **21**: 139–147.

——. 1926. A forest type classification for the Southern Appalachian Mountains and the adjacent plateau and coastal plain regions. (Com. Rpt.) *Jour. Forestry* **24**: 672–684.

——. 1940. Forest cover types of the eastern United States. (Com. Rpt.) 39 pp. Soc. Amer. Foresters, Wash., D. C.

——. 1944. Forestry terminology: A glossary of technical terms used in forestry. (Com. Rpt.) 84 pp. Soc. Amer. Foresters, Wash., D. C.

——. 1945. Forest cover types of western North America. (Com. Rpt.) 35 pp. Soc. Amer. Foresters, Wash., D. C.

Spaeth, J. N. 1934. A physiological study of dormancy in Tilia seed. *Cornell Agr. Expt. Sta. Mem.* **169**. 78 pp.

Sparhawk, W. N. 1918. Effect of grazing upon western yellow pine reproduction in central Idaho. *U. S. Dept. Agr. Bul.* **738**. 31 pp.

Spoehr, H. A. 1926. Photosynthesis. 393 pp. The Chemical Catalog Co., New York.

——, and J. H. C. Smith. 1936. The light factor in photosynthesis. *In* Biological Effects of Radiation, pp. 1015–1058. Ed. by B. M. Duggar. 2 vols., 1343 pp. McGraw-Hill Book Co., New York.

Stahl, E. 1900. Der Sinn der Mycorhizenbildung. *Jahrb. Wiss. Bot.* **34**: 539–668.

Stålfelt, M. G. 1921. Till kännedomen om förhallandet mellan solbladens och skuggbladens kolhydratsproduktion. (Zur Kenntnis der Kohlenhydratproduktion von Sonnen- und Schattenblättern.) *Meddel. Statens Skogsförsöksanst.* **18**: 221–275. (German summary, pp. 276–280.)

——. 1925. Untersuchungen zur ökologie der Kohlensäureassimilation der Nadelbäume. *Meddel. Statens Skogsförsöksanst.* **21**: 249–258.

——. 1931. Die physiologisch-ökologischen Bedingungen der Kronenreinigung. Schaftreinigung und der natürlichen Bestandesreinigung der Fichte. *Skogsvårdsfor. Tidskr.* **29**: 1–44.

STEVENS, C. L. 1931. Root growth of white pine (*Pinus strobus* L.) *Yale Univ. School Forestry Bul.* **32.** 62 pp.

STEWART, G. R. 1933. Forest plantations injured by roosting birds. *Jour. Forestry* **31**: 421–423.

STEWART, W. D., and J. M. ARTHUR. 1934. Some effects of radiation from a quartz mercury vapor lamp upon the mineral composition of plants. *Boyce Thompson Inst. Contrib.* **6**: 225–245.

STICKEL, P. W. 1928. Physical characteristics and silvicultural importance of podsol soil. *Ecology* **9**: 176–187.

STILES, W. 1925. Photosynthesis: The assimilation of carbon by green plants. 268 pp. Longmans, Green & Co., London.

STOCKER, O. 1923. Klimamessungen auf kleinstem Raum an Wiesen-, Wald- und Heidepflanzen. *Ber. Deut. Bot. Gesell.* **41**: 145–150.

STODDARD, H. L. 1931. The bobwhite quail: Its habits, preservation and increase. 559 pp. Charles Scribner's Sons, New York.

STOKLASA, J. 1927. The significance of bacteria in soil productivity. *Abs. 1st Internatl. Cong. Soil Sci., Wash., D. C., Comm. III*, pp. 6–9.

STONE, G. E. 1914. Electrical injuries to trees. *Mass. Agr. Expt. Sta. Bul.* **156.** 19 pp.

STRASBURGER, E., et al. 1930. Strasburger's text-book of botany. Rewritten by H. FITTING, H. SIERP, R. HARDER, and G. KARSTEN. (6th Eng. ed. trans. from 17th German ed. by W. H. LANG.) 818 pp. Macmillan and Co., London.

SUNDLING, H. L., A. C. MCINTYRE, and A. L. PATRICK. 1932. Effect of soil reaction on the early growth of certain coniferous seedlings. *Jour. Amer. Soc. Agron.* **24**: 341–351.

SUTCLIFFE, R. C. 1940. Meteorology for aviators. 276 pp. Chemical Publishing Co., Inc., Brooklyn, N. Y.

TAMM, O. 1920. Markstudier i det nordsvenska barrskogsområdet. (Bodenstudien in der nordschwedischen Nadelwaldregion.) *Meddel. Statens Skogsförsöksanst.* **17**: 49–277. (German summary, pp. 277–300.)

TANSLEY, A. G., editor. 1911. Types of British vegetation. By members of the central committee for the survey and study of British vegetation. 416 pp. Cambridge (Eng.) Univ. Press.

——. 1923. Practical plant ecology: a guide for beginners in field study of plant communities. 230 pp. G. Allen & Unwin, Ltd., London.

——, and T. F. CHIPP. 1926. Aims and methods in the study of vegetation. 383 pp. British Empire Vegetation Committee and Crown Agents for Colonies, London.

TASHIRO, S. 1912. New method for detecting vitality of seeds. *Orig. commun., 8th Internatl. Cong. Appl. Chem.* **26**: 163.

TAYLOR, R. F. 1937. A tree classification for lodgepole pine in Colorado and Wyoming. *Jour. Forestry* **35**: 868–875.

TAYLOR, W. P. 1935. Ecology and life history of the porcupine (*Erethizon epixanthum*) as related to the forests of Arizona and the southwestern United States. *Univ. Ariz. Biol. Sci. Bul.* 3. 177 pp.

——. 1935. "Man and Nature"—a contemporary view. *Sci. Mo.* **41**: 350–362.

——. 1935. Significance of the biotic community in ecological studies. *Quart. Rev. Biol.* **10**: 291–307.

——. 1935. Some animal relations to soils. *Ecology* **16**: 127–136.

——. 1936. Some effects of animals on plants. *Sci. Mo.* **43**: 262–271.

THOMSON, W. G. 1940. A growth rate classification of southwestern ponderosa pine. *Jour. Forestry* **38**: 547–553.

THORNTHWAITE, C. W. 1931. The climates of North America according to a new classification. *Geogr. Rev.* **21**: 633–655.

TOUMEY, J. W. 1895. Vegetal dissemination in the genus *Opuntia*. *Bot. Gaz.* **20**: 356–361.

——. 1903. The relation of forests to stream-flow. *U. S. Dept. Agr. Yearbook*, pp. 279–288.

——. 1919. The relation of gray birch to the regeneration of white pine. *Jour. Forestry* **17**: 15–20.

——. 1921. Damage to forests and other vegetation by smoke, ash, and fumes from manufacturing plants in Naugatuck Valley, Conn. *Jour. Forestry* **19**: 367–373.

——. 1929. Initial root habit in American trees and its bearing on regeneration. *Internatl. Cong. Plant Sci. Ithaca, N. Y., 1926, Proc.* **1**: 713–728. G. Banta Pub. Co., Menasha, Wis.

——. 1929. The vegetation of the forest floor; light versus soil moisture. *Internatl. Cong. Plant Sci. Ithaca, N. Y., 1926, Proc.* **1**: 575–590. G. Banta Pub. Co., Menasha, Wis.

——. 1930. The site factors in the interpretation of forest vegetation. *Verhandl. Internatl. Kong. Forstl. Versuchsanst. Stockholm 1929*, pp. 381–386.

——, and R. KIENHOLZ. 1931. Trenched plots under forest canopies. *Yale Univ. School Forestry Bul.* **30**. 31 pp.

——, and C. F. KORSTIAN. 1942. Seeding and planting in the practice of forestry. 3rd Ed. 520 pp. John Wiley & Sons, New York.

——, and E. J. NEETHLING. 1923. Some effects of cover over coniferous seedbeds in southern New England. *Yale Univ. School Forestry Bul.* **9**. 39 pp.

——, and E. J. NEETHLING. 1924. Insolation, a factor in the natural regeneration of certain conifers. *Yale Univ. School Forestry Bul.* **11**. 63 pp.

TRANSEAU, E. N. 1905. Forest centers of eastern America. *Amer. Nat.* **39**: 875–889.

——. 1908. Relation of plant societies to evaporation. *Bot. Gaz.* **45**: 217–231.

TROUP, R. S. 1928. Silvicultural systems. 199 pp. Clarendon Press, Oxford.

TURESSON, G. 1925. The plant species in relation to habitat and climate. *Hereditas* **6**: 147–236.

——. 1930. The selective effect of climate upon plant species. *Hereditas* **14**: 99–152.

URSPRUNG, A. 1917. Über die Stärkebildung im Spektrum. *Ber. Deut. Bot. Gesell.* **35**: 44–69.

U. S. DEPT. AGR., FOREST SERVICE. 1925. Instructions for making timber surveys in the national forests, including standard classification of forest types. 45 pp. Wash., D. C.

VEIHMEYER, F. J. 1927. Some factors affecting the irrigation requirements of deciduous orchards. *Hilgardia* **2**: 125–284.

——, and A. H. Hendrickson. 1927. Soil moisture conditions in relation to plant growth. *Plant Physiol.* **2**: 71–82.

——, and A. H. Hendrickson. 1928. Soil moisture at permanent wilting of plants. *Plant Physiol.* **3**: 355–357.

——, and A. H. Hendrickson. 1931. The moisture equivalent as a measure of field capacity of soil. *Soil Sci.* **32**: 181–193.

——, and A. H. Hendrickson. 1934. Some plant and soil-moisture relations. *Amer. Soil Survey Assoc. Bul.* **15**: 76–80.

——, J. Oserkowsky, and K. B. Tester. 1928. Some factors influencing the moisture equivalent of soils. *First Internatl. Cong. Soil Sci.* (*1927*) **1**: 513–534.

Vermeule, C. C. 1900. The forests of New Jersey: Forests and water-supply. *In* Ann. Rpt. State Geol., Geol. Survey N. J. 1899, pp. 137–166.

Vesque, J. 1878. De l'influence de la température du sol sur l'absorption de l'eau par les racines. *Ann. Sci. Nat., Bot. 6e série, t.* **6**: 169–201.

Volkens, G. 1887. Die Flora der Aegyptisch-Arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen. 156 pp. Gebrüder Borntraeger (Ed. Eggers), Berlin.

——. 1890. Ueber Pflanzen mit lackirten Blättern. *Ber. Deut. Bot. Gesell.* **8**: 120–140.

Wagner, C. 1923. Die Grundlagen der räumlichen Ordnung im Walde. 4 Aufl. 387 pp. H. Laupp'schen Buchhandlung, Tübingen.

Wahlenberg, W. G. 1946. Longleaf pine: Its use, ecology, regeneration, protection, growth, and management. 429 pp. Charles Lathrop Pack Forestry Found., Wash., D. C.

Waksman, S. A. 1932. Principles of soil microbiology. 2nd Ed. 894 pp. Williams & Wilkins Co., Baltimore.

——. 1936. Humus: Origin, chemical composition, and importance in nature. 494 pp. Williams & Wilkins Co., Baltimore.

Walker, F. A. 1870. Statistical atlas of the United States based on the results of the 9th census, 1870 — Forests. Washington, 1870. (60 cm.)

Walter, H. 1927. Einführung in die allgemeine Pflanzengeographie Deutschlands. 458 s. Gustav Fisher, Jena.

Wang, F. 1890. Fortschritt und Erfolg auf dem Gebiete der Wildbachverbauung. 29 s. K. K. Ackerbauministeriums, Wien.

Warburg, O. 1919. Über die Geschwindigkeit der photochemischen Kohlensäurezersetzung in lebenden Zellen. *Biochem. Ztschr.* **100**: 230–270.

Warburg, P., and E. Negelein. 1923. Über den Einfluss der Wellenlänge auf den Energieumsatz bei der Kohlensäureassimilation. *Ztschr. Phys. Chem.* **106**: 191–218.

Ward, R. DeC. 1913. The influence of forests upon climate. *Pop. Sci. Mo.* **82**: 313–331.

——. 1925. The climates of the United States. 518 pp. Ginn & Co., New York.

Warming, E. 1909. Oecology of plants (Eng. trans. by P. Groom and I. B. Balfour.) 422 pp. Clarendon Press, Oxford.

Warren, E. R. 1926. A study of the beaver in the Yancey region of Yellowstone National Park. *Roosevelt Wild Life Ann.* **1**(1–2): 13–191.

——. 1926. Notes on the beaver colonies in the Longs Peaks region of Estes Park, Colorado. *Roosevelt Wild Life Ann.* **1**(1–2): 193–234.

WEAVER, J. E. 1919. The ecological relations of roots. *Carnegie Inst. Wash. Pub.* **286.** 128 pp.

——, and F. E. CLEMENTS. 1938. Plant ecology. 2nd Ed. 601 pp. McGraw-Hill Book Co., New York.

——, and J. W. CRIST. 1924. Direct measurement of water loss from vegetation without disturbing the normal structure of the soil. *Ecology* **5**: 153–170.

——, and J. KRAMER. 1932. Root system of *Quercus macrocarpa* in relation to the invasion of prairie. *Bot. Gaz.* **94**: 51–85.

WEBER, R. 1903. Die Aufgaben der Forstwirtschaft (*In* Lorey's Handbuch der Forstwissenschaft), Bd. I, s. 1–102. Verlag der H. Laupp'schen Buchhandlung, Tubingen.

WEED, C. M., and N. DEARBORN. 1903. Birds in relation to man. 380 pp. J. B. Lippincott Co., Philadelphia.

WEIR, J. R. 1916. Mistletoe injury to conifers in the Northwest. *U. S. Dept. Agr. Bul.* **360.** 39 pp.

——, and E. E. HUBERT. 1919. A study of the rots of western white pine. *U. S. Dept. Agr. Bul.* **799.** 24 pp.

WEIS, F. 1932. Fortsatte Fysiske og kemiske Undersøgelser over Danske Hedejorder og andre Podsoldannelser [Further investigations on Danish heath soils and other podsols]. *K. Danske Vidensk. Selsk., Biol. Meddel.* **10**(3): 1–202.

WELLS, B. W., and I. V. SHUNK. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina coastal plain: An ecological study. *Ecological Monog.* **1**: 465–520.

WERTH, E. 1927. Klima- und vegetations- Gliederung in Deutschland. *Mitt. Biol. Reichanst. Land- u. Forstw.* **33**: 1–40.

WESTVELD, R. H. 1933. The relation of certain soil characteristics to forest growth and composition in the northern hardwood forest of northern Michigan. *Mich. Agr. Expt. Sta. Tech. Bul.* **135.** 52 pp.

——. 1939. Applied silviculture in the United States. 567 pp. John Wiley & Sons, New York.

WHERRY, E. T. 1920. Soil acidity and a field method for its measurement. *Ecology* **1**: 160–173.

——. 1922. Soil acidity: Its nature, measurement, and relation to plant distribution. *Smithsn. Ann. Rpt. 1920, Pub.* **2630,** pp. 247–268.

——. 1922. Soil acidity preferences of some eastern conifers. *Jour. Forestry* **20**: 488–496.

WIESNER, J. 1872. Ueber den Einfluss hoher Temperaturen auf die keimfähigkeit einiger Samen. *Landw. Vers. Sta.* **15**: 297–299.

——. 1876. Untersuchungen über den Einfluss des Lichtes und der strahlenden Wärme auf die Transpiration der Pflanze. *Sitzber. Akad. Wiss. Wien. Abt. 1.* **84**: 477–531.

——. 1907. Der Lichtgenuss der Pflanzen; photometrische und physiologische Untersuchungen mit besonderer Rücksichtnahme auf lebenweise, geographische Verbreitung und Kultur der Pflanzen. 322 s. W. Engelmann, Leipzig.

WILDE, S. A. 1934. Soil reaction in relation to forestry and its determination by simple tests. *Jour. Forestry* **32**: 411–418.

——. 1946. Forest soils and forest growth. 241 pp. Chronica Botanica Co., Waltham, Mass.

WILLSTÄTTER, R. M., and A. STOLL. 1918. Untersuchungen über die assimilation der Kohlensäure. 448 s. J. Springer, Berlin.

WILSON, J. D., and B. E. LIVINGSTON. 1932. Wilting and withering of grasses in greenhouse cultures as related to water-supplying power of the soil. *Plant Physiol.* **7**: 1–34.

WISLICENUS, H., and F. W. NEGER. 1914. Experimentalle Untersuchungen über die Wirkung der Abgassäuren auf die Pflanze. *Mitt. K. Sächs. Forstl. Versuchsanst. zu Tharandt* **1**: 85–233. Paul Parey, Berlin.

WOEIKOF, A. 1885. Der Einfluss der Wälder auf das Klima. *Petermann's Mitt. Justus Perthes' Geogr.* **31**: 81–87.

——. 1889. Einfluss einer Schneedecke auf Boden, Klima and Wetter. *Geogr. Abhandl.* **3**: 3.

WOODHEAD, T. W. 1906. Ecology of woodland plants in the neighborhood of Huddersfield. *Jour. Linn. Soc. [London], Bot.* **37**: 333–406.

——. 1919. History of the vegetation of the southern Pennines. *Jour. Ecology* **17**: 1–34.

——. 1928. The forests of Europe and their development in post-glacial times. *Empire Forestry Jour.* **7**: 168–184.

WOODWARD, K. W. 1913. Use of forest types in the work of acquiring land under the Weeks Law. *Soc. Amer. Foresters Proc.* **8**: 69–72.

YAPP, R. H. 1922. The concept of habitat. *Jour. Ecology* **10**: 1–17.

YOUNG, H. E. 1936. A mycorrhizae-forming fungus of *Pinus*. *Jour. Aust. Inst. Agr. Sci.* **2**: 32–34.

ZACHAROWA, T. M. 1925. Über den Einfluss niedriger Temperaturen auf die Pflanzen. *Jahrb. Wiss. Bot.* **65**: 61–87.

ZEDERBAUER, E. 1907. Das Lichtbedürfnis der Waldbäume und die Lichtmessmethoden. *Centbl. Gesam. Forstw.* **33**: 325–330.

——. 1912. Versuche über individuelle Auslese bie Waldbäumen. *Centbl. Gesam. Forstw.* **38**: 201–212.

ZELLER, S. M. 1920. Humidity in relation to moisture imbibition by wood and to spore germination on wood. *Ann. Missouri Bot. Gard.* **7**: 51–73.

ZILLICH, R. 1926. Über den Lichtgenuss einiger Unkräuter und Kulturpflanzen. *Landw.* **1**: 461–471.

ZON, R. 1906. Principles involved in determining forest types. *Soc. Amer. Foresters Proc.* **1**: 179–189.

——. 1913. The relation of forests in the Atlantic plain to the humidity of the Central States and prairie region. *Soc. Amer. Foresters Proc.* **8**: 139–153.

——. 1915. Seed production of western white pine. *U. S. Dept. Agr. Bul.* **210**. 15 pp.

——. 1920. Forests and human progress. *Geogr. Rev.* **9**: 139–166.

——. 1927. Forests and water in the light of scientfic investigation. *Reprinted from App. V., Final Rpt. Natl. Waterways Comn. 1912.* 106 pp. (*Senate Doc. 469, 62nd Cong., 2nd Sess.*)

——, and H. S. GRAVES. 1911. Light in relation to tree growth. *U. S. Dept. Agr., Forest Serv. Bul.* **92**. 59 pp.

INDEX

Acclimatization, 48
Acidity, forest soil, 92
Adjustments to control, water intake, 141
  water loss, 138
Aeration, soil, 114
Aesthetics, forest, 236
After-ripening of tree seed, 256, 273
Age, effect, on bole form, 248
  on crown form, 247
Agriculture, 179
Air currents, effect of forests on, 221
Air masses, 64
  characteristics of, 64
  of the United States, 65
  sources of, 64
Algae in soil, 100
Alternation, 403
Altitude, 155–157
  effect, on tolerance, 348
    on trees, 155–156
  modifying geographic climate, 155
Animals, effects of forest on, 229–238
  effects on forest, 171
  forests, as environments for, 230
    as source of food for, 229
  introduction of, 179
  law of dispersion of, 231
Anthropeic site factors, 11
Aridity, relation to vegetative period, 52
Ash constituents of soil, 95
Assimilation, rate of, proportional to light intensity, 18
Association, forest, 377
Atmosphere, humidity in, 57–61
  impurities in, 78
    resistance to, 79
  moisture in, 50–62
Attrition, forest fires causing, 181
Avalanches, 56, 159, 224
  effect of forests on, 159, 224
  kind of, 224
Azotobacter in forest soil, 101

Bacteria, 100
  effect of soil acidity on, 102
  relation to forest soil fertility, 102
  role in soil respiration, 102
Beaver, 174
Biotic factors, 12, 164–181
Birds, 176
Bole, 247
  cross-sectional form of, 248
  crotched or double-topped, 251
  defects in, 249
  effect of external influences on, 250
  excellencies in, 249
  form of, 247
  inherent characteristics of, 249
  relation, to growing space, 248
    to site, 249
  straightness of, 247
  taper of, 248
    change in, 270
Branches, epicormic, 251
Brewer's classification of forests, 359
Browsing, selective, by deer, 172, 174

Cajander's method of site determination, 9
Cajander's system of indicator types, 392
Cambium, activity of, 40
Canopies, artificial, 336
  living, effect on vegtation of forest floor, 338
  natural, 336
Carbon dioxide in forest air, 78
Chlorosis, 116, 118
  cause of, 118
Civilization, influence of forests on, 233
Clay in soils, 89
Clements' classification of vegetation, 368
Climate, 63–79

Climate, importance of, in forestry, 63
modified by altitude, 155
periodicity in, 68
Climatic factors, 11
integration, 69
Climatic provinces, 69
Climax stage in succession, 416
Cold, injurious effects of, 41
Colloids in soils, 89
Commensalism, 168
Competition, 164, 412
for moisture, 338, 413
how expressed, 164
importance of, 414
Consociation, 378
Coppice, 252, 260, 316
Cover types, 382, 385–392
application of, 385
regional classification of, in United States, 386
Cross-breeds, 244
Crown, form of, 245
Crown classification, for even-aged stands, 304
for uneven-aged stands, 306
Crown closure, degree of, 299
importance of, 301
influence, on growth, 303
on soil, 304
on stand, 301
Crown density, conditions which influence, 301
Crown position, classification based on, 304

Damping-off, 169
Deer, 174
Dendrology, biological, 1
Development, 254, 411
Dew, 51
Dew-point, 51
Dormancy in trees, 256, 274
Drought, 52, 69, 100, 160, 167, 191, 213, 216, 220, 258
resistance, 12
Dryness, physiological, 59
Dunning's tree classification for uneven-aged stands, 306

Earth, configuration of, 154
Earthworms, effect on soil, 107
Ecological optimum, 42, 186
Edaphic factors, 12
Elk, 174
Energy, radiant, transformation of, 18
value, in different parts of visible spectrum, 26
Environment, influence of forests on, 193–238
Epicormic branches, 251
Epidermal outgrowths, variations in, 140
Erosion, 226–228
control, 228
damage from, 226–228
Establishment, 403, 408
Evaporation, 61, 207
effect of forest on, 207
from ground, 210
from saturated soil, 211
from tree crowns, 208
in the forest, 210
Exposure, direction of, 159

Factors, biological, affecting soil structure, 108
biotic, 12, 164–181
classification of, 13
climatic, 11, 63–79
combined action of, 182–192
compensating, law of, 184
indirect physiographic, 154
limiting, principles of, 188
maximum value, 189
measuring effectiveness of, 182
minimum value, 189
origin of, 10
physiographic, 12, 154–163
significance of, 186
sources of, 10
varying influence of, 183
virgin forests adjusted to, 183
Field capacity of soil, 123, 124
Fillers, 298
Fire, 180
effect, on forest succession, 397
on reproduction, 326
in forest, 180
Floods, influence of forests on, 220
Forest, effect, on air currents, 221

Forest, effect, on amount of absorbing medium, 216
on animal life, 229–238
on erosion, 226–228
on evaporation, 210
on floods, 220
on man, 232
on pathogenic microbes, 234
on precipitation, 204
on runoff, 213
on seepage, 215
on soil, 226
on springs, 216
on stream flow, 217
on temperature, 194–201
on tranquillity of mind, 236
on transpiration loss, 212
on water conservation, 207–220
on water retention, 215
on weather, 234
on wind erosion, 226
indirect value of, 193
influences, 193–238
life history of, 396
Forest aesthetics, 236
Forest association, 377
Forest communities, 179, 373
of varying degrees of magnitude, 373
origin and development, 396–417
Forest floor, 94
Forest regions, *see also* Vegetation, classification of
of United States, 362
sanitary influence of, 233
succession, *see* Succession
types of, *see* Types, forest
vegetation, *see* Vegetation, forest
Form factor, 247
Formation, forest, 373
Freezing, soil, effect of forest vegetation on, 201
Fronts, weather, 66
Frost, causes of injury from, 43
heaving in nurseries, 110
injury, 41, 44
variation with age of tree, 46
resistance of trees to, 43
resistance to, in dormant season, 43
in growing season, 43

Germination, 409
Glaze, mechanical effect on forests, 56
Gradient, classification of, 158
effect on trees, 158
Grazing, 172, 328
by domestic animals, 172
effect of, 172, 328
on reproduction, 328
selective browsing by deer, 172, 174
Growth, 254
annual height, 265
characteristics of chief importance, 263
determinate, in leading shoot, 264
diameter, 267
effect of age on, 267
variations in different parts of tree, 268
effect, of light intensity on, 23–26
of thinning on, 330
height, 264
and soil characteristics, 98
indeterminate, in leading shoot, 265
in stands, 329
maximum height, 266
quality of, 270
rapidity of, 262
relation to added increments of light, 21
Growth forms, classification of vegetation on, 358
evolution of, 136
in relation to available water, 137
Growth rings, 258
volume, increase in, 270

Habitat, 7
factors, 10
Hail, 51
Hardpan formation in forest soils, 83
Heat, absorption by trees, 40
injurious effects of, 41
transmission by trees, 40
Height growth, 264
variations in, 141
Highs, 65
Humidity, 57, 201
absolute, 59

Humidity, atmospheric, 57, 201
effect of forest on, 201
relative, 57
excess in forest, 203
inside and outside forest, 202
Humus, 93
colloidal nature of, 97
composition, 93
decomposition, 93
effect on forest vegetation, 95
favorable influence of, 96
in forest soil, 93
nutrients in, 95
raw, 95
relation to forest growth, 100
types, forest, 94
Hybrids, 244
Hygroscopic coefficient, 123

Illumination, intensity of, effect on leaf structure, 30
Illuminometer, Macbeth, 21
Impurities, in atmosphere, 78
resistance to, 79
Increment, in stands, 329
volume, 270
Indicator types, 383
application of, 392
Insects, 177
Insolation, effect, on reproduction, 48
on soil temperature, 48
Interrelationships between plants, 166

Law, of dispersion of animals, 231
of physiological limits, 189
Liebig's law of minimum, 187
Mitscherlich's restatement of, 187
Light, 14–38
absorbed by plants, 26
and silvicultural practice, 35
changed in quality in passing through leaves, 26
changed in quality by reflection from leaves and other plant surfaces, 26
daily exposure to, effect on time of flowering and fruiting, 32
duration of, 32
effect, on death of lower limbs of trees in stands, 30
Light, effect, on plant grouping, 401
on preventing the development of foliage in interior of tree crowns, 30
on protoplasm, 30
effects of, 17–18
intensity, and growth, 23–26
and photosynthesis, 18–23
minimum, to balance CO_2 used in photosynthesis, 19–21
phototropic effect of, 31
quality, 26–29
on forest floor, 26
reflected by plants, 26
relation, to elongation of tree axes, 29
to tree form, 29
role of, in forest, 14–38
Lightning, direct effect of, 77
indirect effect of, 77
Litter, effect of, on evaporation from ground, 211
on soil freezing, 201
forest, 94, 163
seed storage in, 112
Locality, 7
Lows, 65
Lumbering, 179, 327
effect, on forest succession, 398
on reproduction, 327

Man, effect of forest on, 232
effect of, on forest, 177–181
Management types, 383, 390
application of, 390
Mayr's classification of forests, 361
Merriam's life zones, 360
Mice, 176
Microbes, effect of forest on, 234
Microorganisms in soil, activity of, 100–107
relation to fertility, 100–107
Migrants, agents for carrying, 405
mobility in, 405
Migration, 404
Minimum, Liebig's law of, 187
Mist, 51
Mitscherlich's law of minimum, 187
Moisture, atmospheric, 50–62
Moisture equivalent, 123, 124
Mor, 94, 107, 116

Mull, 94, 107
Mutualism, 167
Mycorrhizae, 100. 102–106, 166
  ectendotrophic, 103
  ectotrophic, 103
  endotrophic, 103
  prevalence in trees, 103
  role in tree nutrition, 104

Nitrogen, fixation of, 100
  loss from soil, 96
  sources of, 93, 96
  transformations, different in different forest types, 96
Non-ash constituents of soil, 95
Nurse trees, 297
Nutrients, mineral, deficiency in, 92

Occurrence, 281
Organic matter in soil, 93–97
Organs, assimilating variation in illumination of, 140
Orstein, 83
Orterde, 83
Osmosis, 142
Osmotic pressure of plant sap, variations in, 142
Overgrazing, effects of, 173

Pan, formation in forest soils, 83
Parasites, 166, 169
  importance of, 169
  plant, effect on host, 170
Pedalfer soils, 87
Pedocal soils, 87
Percolation of water in soil, 125
Permanent types, 382, 392
  application of, 392
Pests, introduction of, 180
Photoperiodism, 32
Photosynthesis, and light intensity, 18–23
  and minimum light intensity, 18–23
  physiological significance of, 17–23
  relation, of light intensity to, 18
    to light quality, 28
Phototrophic effects, relation to light intensity, 31
Phototropism, 31
Physical types, 382, 391
Physical types, application of, 391
Physiography, 12, 154–163
  progressive changes in, 12
  rhythmic changes in, 12
Physiological limits, law of, 189
Plant grouping, 399
  in relation, to light and moisture, 401
    to structure, 402
  variety in, 400
Plants, interrelationships between, 166
  introduction of, 179
Podsol soils, 83, 117
Porcupines, 176
Precipitation, 51, 67, 127, 209
  effect of forest on, 209
  intercepted by tree crowns, 127, 206, 210
  rate of absorption by soil, 214
  resistance of trees to mechanical injury from, 54
  uneven distribution of, 52
Precipitation-evaporation ratio, 61
Precipitation-vapor pressure deficit, 62
Pyric site factors, 11

Quadrats, effect of trenching on soil moisture in, 129
  trenched, available soil moisture in, 129

Rabbits, 175
Races, 240, 242
Radiant energy, nature of, 14
  summary of, in relation to forest vegetation, 36
Radiation, duration of, and effects, 32
  infra-red, wave lengths of, 15
  solar, 14–38
    altered by earth's atmosphere, 16
    reaching earth's surface, 16
  ultra-violet, wave lengths of, 15
  visible, 14
    wave lengths of, 15
Radiometer, Gast, 342
  Shirley, 343
Rain, 51
Rainfall, 52
Range of species, extension of, 47
  by planting, 47

Reaction, 193, 412, 415
concepts, 193
of forest on site factors, 185
Reactions, classification of, 415
forest, classification of, 194
soil, 415
Reproduction, 271, 317
artificial, 317
continuous and discontinuous, 322
distribution of, under hemlock, 185
effect of fire on, 326
effect of grazing on, 328
effect of lumbering on, 327
natural, 317
from seed, 319
in clearings, 322
origin of, 318
problems of, 322
study of, 325 •
within stands, 324
under natural canopies, 336
under spruce in relation to decayed wood beneath litter, 184
Rest periods in trees, 256
Retrogression of vegetation, 416
Rings, growth, 258
Root closure, 308
influence on stand, 309
Root competition and decline of reproduction under old stands, 336–340
Root form, variations in, 145, 253
Root growth, periodicity in, 257
Root habit, characteristic forms of, 148
initial, forms of, 144
variations in, 144
Root penetration, depth of, 147
Root surface, area of, 143
Root system, 145
initial, correlations in, 147
plasticity in, 145
Roots, duration of growth in, 262
external influences affecting, 253
forms of, 253
inherent characteristics of, 253
longevity and death, 259
periodicity of growth in, 257
rest periods of, 257
Runoff, surface, effect of forest on, 213
Sargent's classification of forests, 359
Saturation deficit, 57
Seed production, 272
Seepage, proportion to runoff, 213
Shoot form, variations in, 141
Shoot surface, area of, 143
Shreve's classification of vegetation, 368
Silvics, 1
Silvicultural practice, and light, 35
effect on soil, 116
Silvicultural systems, 319–321
clear-cutting, methods, 320
patch method, 321
strip method, 321
seed tree, 320
selection, 319
shelterwood, 319
Silviculture, 1
effect of tolerance on, 353
foundations of, 1
practice of, 2
Site, 7
classification, 8
differences in, 10
factors, 10–13
anthropeic, 11
biotic, 12
classification of, 13
climatic, 11
compensating, 175
directly operating, 10
edaphic, 12
effect on forest vegetation, 183
effectiveness of, 182
indirectly operating, 10
interaction of, 182–192
modified by silviculture, 189
physiographic, 12
pyric, 11
significance of, 186
index, 9, 98, 125
quality, 8
Sleet, mechanical effect on forests, 56
Slope, effect on trees, 158
Snow, 51, 53, 55, 161
cover, effect of duration of, on forests, 52
effect of, in forest, 161
Snowbreak, 56
Snowfall, interception of, by tree crowns, 209

Society, plant, 378
Soil, acidity, 97
  aeration, 114
    adjustments to poor, 114
  animal life in, 106, 125
  arrangement of particles, 107
  atmosphere, 113
  bacterial flora of, 101
  base exchange in, 92
  calcification, 85
  capillarity of, 120
  carbonation, 82
  characteristics and height growth, 98
  classification, 86
  clay fraction in, 88
  colloidal content, 89
  composition of, 91–93
  conditions, 80–119
  constituents and availability, 92
  cover, 161
    living, 163
    non-living, 161
  crumb structure, 107
  depth, 91
  development processes, 83
  dynamic nature of, 83
  effect of climate on, 83
  effect of forest fires on, 99, 108
  effect of silvicultural practice on, 116
  fauna, 106
  fertility, maintenance in forest, 116, 118
  freezing, effect of, 110
  fungus flora of, 100
  gases, 113
    toxic, 116
  granulation, 90
  gravel fractions of, 88
  hardpan, 83, 116
  horizons, 81
  hydration, 82
  hydrolysis, 82
  hygroscopicity of, 123
  inorganic chemical nature, 91
  laterization, 84
  mechanical analysis of, 88
  moisture, 120–153
    available, adjustments to, 137
      influence on forest, 135
Soil, moisture, basic concepts, 120
    constants, 123
    effect, on forest vegetation, 120–153
      on plant grouping, 401
    increased by trenching, 129
    in relation to snowfall, 53
    movement, 121
  organic matter, 93–96
  oxidation, 82
  physical properties, 88
  plant life in, 100
  podsolization, 83
  porosity, 125
  profile, 81
  reaction, 97
  sand fractions of, 88
  series, 88
  shrinking and swelling in, 110
  silt fraction of, 88
  solution, 92
  specific gravity, 91
  structure, 89
    and fertility, 107
    in relation to aeration, 113
  surface, temperature of, 112
  temperature, 108–113
    effect of forest on, 198
    effect on forest, 112
    effect on water absorption, 109
    fluctuations in, 111
    in forest and open, 112
    influence on tree form, 111
  texture, 89
  type, 88
  volume weight, 91
  water, loss from, 125
    loss, through evaporation, 126
      through transpiration, 127
    percolation in, 125
  water absorption by trees, 131
  weathering processes, 82
Soils, Pedalfer, 87
  Pedocal, 87
  podsol, 83, 116
Solar radiation, 14–38
Species, 240, 241
  dependent, 288
  frost-resisting power of, 41
  relation, to available soil water, 135
    to critical temperature, 45

Species, relation, to temperature extremes, 42
resistance to wind, 70
Spectral energy distribution, 14
Spectrum, visible, 15
Springs, influence of forests on, 216
Sprout stands, 252, 260, 316
Squirrels, 175
Stand, 275
Stands, age of, 275
composition of, 279, 282
density of, 299, 310
developmental stages in, 276
development of, 311
differences in reaction of, 284
differentiation of, 275
directing composition of, 286
even-aged advantages, 278
artificial mixtures, 296
development of, 311
disadvantages, 279
form, 277
formative ability in, 285
growth of, 329
increment in, 329
mixed, 279–298
advantages of, 290
occurrence in, 281
pure, 279, 287–289
advantages of, 289
reproduction of, 317–328
sprout, 252, 260, 316
temporary mixtures, 298
two-aged artificial mixtures, 297
uneven-aged, development of, 314
yield of, 331
Stem girdle, 112
Stool shoots, 252
Storm paths, 67
Stream flow, 217
amount of water available, 218
Structure of trees, 138, 141
internal, variations in, 138, 141
Succession, climax in, 416
concept of, 396
continuing causes in, 399
direction of, 416
initial causes in, 398
primary, 397
secondary, causes in, 397
Sun scald, 41
Surface, evaporating, variations in area of, 139
land, 161
Symbiosis, 100

Taper of bole, 248, 270
change in, 270
typical forms of, 270
Temperature, adverse, and underplanting, 47
air, 39–49, 194–198
effect of forest on, 194
effect on forest, 40–48
mean daily range of, 197
critical, 43
relation of individuals to, 46
relation of species to, 45
effect, on different plant functions, 42
on forest distribution, 42
on structural modifications in tree trunks, 39
on tolerance, 347
on tree form, 39
on vital processes, 39
effect of forest on, 194–198
effects, 33–35
limiting factor, 43
lower critical, 43
relation, to assimilation, 43
to species distribution, 42
soil, 108–113
effect of forest on, 198
effect on forest, 112
surface soil, 112, 200
Temperatures, critical, for forest trees, 43–47
Temporary types, 382, 392
application of, 392
Thermopile, Coblentz, 20
Thinning, effect on growth, 330
Timberline, 42, 67
Tolerance, 336–355
apparent, 347
concepts of, 336
definitions of, 341
factors influencing, 347
importance in silviculture, 353
methods of determining, 341
scales of, 349

Topography, 154
effect on migration, 408
Transpiration, effect of forest on, 212
rate of, 212
Trees, 239–274
as individuals, 239–274
crotched or double-topped, 251
determining age of, 258, 261
effect of early frosts on, 39
effect of late frosts on, 39
fat storing, 39
form of, 236
growth of, 254
heat requirements of, 33
longevity and death of, 259
maximum height of, 266
prostrate forms, 40
rest periods in, 256
structures and functions of, 239
Trenching in forest, 129, 338
effect on soil moisture, 130, 213, 338
Types, forest, 379–395; *see also* Vegetation, classification of
concepts of, 380
delimiting, 395
mapping of, 395
regional classification of, in United States, 386
relation to ecological units, 383

United States Forest Service classification of forests, 362

Vapor pressure deficit, 57, 62
Varieties, 240, 241
Vegetation, classification of, 356–395
classification on basis of growth form, 358
ecological aspects of, 8
effect of site factors on, 183
forest, in United States, 359
on ecological basis, 365
on non-ecological basis, 359
regional classification, in United States, 362
natural, 358, 365
resultant of complex of factors, 188

Water, absorption of, by trees, 131
adsorbed in soil, 120
Water, amount in soil, 132
and vital processes in trees, 50
available, fluctuations in, 134
capillary, 120
gravitational, 120
ground, 120
hydration, 120
hygroscopic, 121
in forest soils, 132
in soil, available, 132
average at different depths, 128
loss, through evaporation, 126
through transpiration, 127
seasonal variation in, 128
unavailable, 133
intake, adjustments to control, 141
interstitial, 120
loss, adjustments to control, 138
percolation in soil, 125
potable, effect of forests on, 235
relations, dynamics of, 137
sprouts, 251
Water-supplying power of soil, 123, 124
Weather, 63, 64
importance of, in forestry, 63
Weathering, chemical, 82
physical, 82
soil, a product of, 82
Wetness, physiological, 59
Wilting coefficient, 123, 124
Wilting percentage, 123
Wind, 71–76, 247, 250, 269
breakage from, 72
continuous stress caused by, 72
direct action of, 71
effect on forest distribution, 75
erosion, effect of forest on, 226
in the forest, 71
indirect effect of, 74
mechanical action on trees, 71, 247, 250, 268
utility of, to trees, 75
velocity, 74
Windbreak, 72
Windbreaks, 221–224
effect of, 211, 221
on air temperature, 223
on soil moisture, 222

Windbreaks, efficiency of, 223
Windfall, 72
  damage from, 73
Winter hardiness, 12

Xerophyte, 59

Yield, factors affecting, 332
  of stands, 331

Zonation, 129, 402
  vertical, in forest, 129
Zon's classification of forests, 370